# MID-TERTIARY CYTHERETTINAE OF NORTH-WEST EUROPE 

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# MID-TERTIARY CYTHERETTINAE OF NORTH-WEST EUROPE 

By M. C. KEEN

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## SUMMARY

Fifty eight species and subspecies of Cytheretta and ten of Flexus are described from the Middle and Upper Eocene and the Oligocene of western Europe. New species and subspecies are: from the Bartonian of the Paris Basin, Cytheretta costellata grandipora, C. costellata cratis, C. carita, C. cellulosa, C. ruelensis, and Flexus ludensis; from the Upper Eocene of the Hampshire

Basin, C. costellata antecalva, C. forticosta, C. porosacosta, $F$. solentensis solentensis and $F$. solentensis congestus; from the Oligocene of the Paris Basin, C. tenuipunctata absoluta, C. tenuipunctata livata, C. tenuistriata ornata, C. minipunctata, C. buttensis buttensis, C. buttensis reticulata, C. posticalis parisiensis, C. vesca, and C. stigmosa gallica; and from the Oligocene of the Aquitaine Basin, C. oligocaenica, C. regularis, C. bullans, C. gibberis, C. sagri inconstans, C. sagri martini, C. minipustulosa, C. postornata, and $F$. lenijugum. The stratigraphical distribution, ecology, and classification are also discussed.

## I. INTRODUCTION AND ACKNOWLEDGMENTS

THE following study of the subfamily Cytherettinae is mainly concerned with Upper Eocene and Oligocene species, but also includes some from the Lutetian, from possible Miocene, and from the Pliocene and Recent. The area covered includes the Hampshire Basin, the Paris Basin, Belgium and the Aquitaine Basin.

The study is taken from a Ph.D. thesis completed at the University of Leicester in 1967. Since then the Geology Department has had a scanning electron microscope installed, and through the permission of Prof. P. C. Sylvester-Bradley it has been possible to re-photograph the ostracods. This has sometimes brought out characters which are not very clear under an optical microscope, and very high magnifications are possible which show features not visible at all with an ordinary microscope. The photographs were taken by Mr G. Mc. Turk, to whom thanks are extended.

The stratigraphy of the Upper Eocene and Oligocene in Western Europe is complicated but the nomenclature of the stage names is even more so. There are some thirteen of the latter in common usage between the Lutetian and the Chattian, so to avoid confusion formation names are used where possible. When stage names are used however, they refer to the current usage in the particular area under discussion. When two or more areas are mentioned, the classification adopted is that of Wrigley \& Davis (1937). Recent reviews of the stratigraphy can be seen in Batjes (I959), Cavelier (I964, I965), Curry (I965, I966), and Vigneaux (I964).

There are three main problems for the correlation of the mid-Tertiary within western Europe. The first is the relationship between the Middle and Upper Eocene; the second is the difficulty of recognizing the Bartonian in Belgium and the Paris Basin; and finally the placing of the Eocene-Oligocene boundary. Recent symposia at Bordeaux (1962), Paris (1968), and Marburg (1969) have failed to adopt any firm conclusions on any of these points. Most of the traditional concepts are under debate, and with so many ideas in the air correlation charts become redundant very quickly. Fig. I lists the horizons sampled for Cytheretta and also gives a tentative correlation.

The species concept adhered to in this work is narrower than has perhaps been usual with Tertiary ostracods. The reasons for this are, first, that by studying one subfamily it is possible to follow its geographical and stratigraphical ramifications. Secondly, comparisons have been made with type material whenever possible. Finally, it is my belief that it is only through the detailed studies of small groups of ostracods that they will take their rightful place for use in Tertiary stratigraphical correlation.

| $\begin{aligned} & \text { MIDDLE } \\ & \text { EOCENE } \end{aligned}$ | $\begin{aligned} & \text { UPPER } \\ & \text { EOCENE } \end{aligned}$ |  |  | OLIGOCENE |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & 0 \\ & < \\ & 0 \\ & 0 \\ & m \end{aligned}$ |  |  | $\begin{aligned} & 0 \\ & D \\ & 0 \\ & \sim \\ & 0 \\ & \infty \\ & \sim \\ & \sim \end{aligned}$ |
|  | $\begin{aligned} & \square \\ & n \\ & \xrightarrow[n]{\square} \\ & \xrightarrow[n]{n} \end{aligned}$ |  |  |  | $$ |
|  |  |  |  |  | $\begin{array}{ll}  & I \\ & D \\ \infty & \leq \\ D & 0 \\ \sim & \backsim \\ \sim & I \\ Z & D \\ & m \end{array}$ |
|  | $\begin{aligned} & m \\ & O \\ & N \\ & D: \\ & Z \\ & 1<1 \end{aligned}$ |  |  |  |  |
|  | $\begin{aligned} & \infty \\ & \stackrel{\infty}{m} \\ & \stackrel{m}{m} \\ & \stackrel{m}{n} \end{aligned}$ |  | $\begin{aligned} & 3 \\ & D \\ & Z_{D}^{D} \\ & \sum_{M} \end{aligned}$ |  |  |

Fig. I. Correlation of Mid-Tertiary Beds in western Europe.

I should like to record my grateful thanks to Prof. P. C. Sylvester-Bradley for his supervision throughout the work and for the use of the facilities of the Department of Geology at the University of Leicester. A study such as this also needs the cooperation of researchers in other countries, and I should particularly like to thank Dr H. J. Oertli, Mlle B. Deltel, the late Prof. J. Cuvillier, and Mme R. Damotte in France; Dr P. Marks in Holland; and Dr E. Triebel in Germany. The work was made possible by a N.E.R.C. NATO Research Studentship. The text-figures have been drawn by Mrs N. Farquharson.

The ostracods described in this paper are in the collections of the British Museum (Nat. History) Palaeontology Department.

## II. LOCALITIES

Most of the samples used came from classical localities, either collected personally or donated by other workers. The sections are often poorly exposed, so few detailed measurements were taken. The relevant parts of some of the sections are given below. Other localities can be seen in Fig. 2.

1. Cormeilles-en-Parisis (P.C.M.).

This famous locality situated in the western suburbs of Paris reveals strata ranging from the marnes à L. inornata, through the gypsum beds, to the Couches de Sannois and Marnes à Huîtres at the top.
P.C.M.I8-23; Couches de Sannois, sandy clays with shell bands. The samples come from beds $40,42,44,45,46$, and 47 respectively of Albissin (1955).
P.C.M.24; basal Marnes à Huîtres.
P.C.M.25; sandy clay 115 cm above base.
P.C.M.26; oyster bed 230 cm above base.
P.C.M.27; Brown clay with Polymesoda immediately above oyster bed.
2. Moiselles (PMS)

A sand pit beside the RN I some twenty miles north of Paris. Sables de Beauchamp, Sables d'Ezanville, and Calcaire de St. Ouen are exposed. Only one sample, PMS.8, has yielded well preserved Cytheretta species; this is from the Sables de Beauchamp, 480 cm below the base of the Sables d'Ezanville.

## 3. Marnes à P. ludensis of the Paris Basin.

Two localities yielded ostracods: Chavençon and Verzy. At both localities the Marnes à $P$. ludensis is thin; about 150 cm at Chavençon, PCC.I near the base, PCC. 2100 cm above; about 90 cm at Verzy, PVY. 2 at base, PVY. 340 cm higher, PVY. 430 cm higher still.


Fig. 2. Localities sampled for Cytherettinae.
4. Biarritz (RO).

The cliff section at Biarritz exposes strata ranging from the Lutetian to the upper part of the Oligocene. Cytheretta species are described from the following samples, collected at the foot of the cliffs. No detailed section was measured.

RO 264; base of the Couches de l'Atalaye.
RO 265 ; entrance to the tunnel at the Musée de la Mer.
RO 266; southern end of the Grande Plage.
RO 267; Rochers de la Villa Eugenie.
RO 268; southern end of the Falaise lou Cout.
RO 269, 270, 271 ; in ascending order below the Phare St Martin, collected over about io m of strata.
5. Other localities in the Aquitaine Basin.
(a) Bartonian clays of Lespontes.
(b) Stampian of Gaas. Two localities were sampled, Espibos (AGE) and Lesbarritz (AGL). The former of these is a completely overgrown quarry, where two samples were collected by digging, AGE. I being slightly lower on the slopes than AGE.2. At Lesbarritz, AGL.I was from the cream marls exposed at the base of the section below the coral horizon.
(c) St Geours de Maremne. The controversial locality at Escornbéou, which is of topmost Oligocene or lowermost Miocene age.
6. Headon Beds of the Hampshire Basin.

About roo samples were examined; all cytherettinid species come from the Middle Headon Beds. Samples mentioned in the text are: Headon Hill, EHH. 42 , coming 165 cm above the base of the Venus Bed; Whitecliff Bay, EWB(A) from the base of the Brockenhurst Beds, $\mathrm{EWB}(\mathrm{B})$ to cm higher, EWB. 19 from roo cm above the top of the Barren Sands, and EWB. 22100 cm above EWB.Ig. Other localities sampled are Colwell Bay, Milford, and Brockenhurst.
7. Other localities.

Bracklesham Beds of Selsey Bill, Whitecliff Bay, and Bramshaw.
Auversian of Auvers-sur-Oise, and Le Ruel.
Stampian of Auvers-St-George, St Cloud, Ormoy, and Morigny in the Paris Basin, and of Weinheim Trift in the Mainz Basin.

Upper Oligocene of Astrup, near Osnabruck.
Ledian of Bambrugge, Belgium.

## III. STRATIGRAPHICAL DISTRIBUTION

The genus Cytheretta is probably the commonest ostracod genus found in the midTertiary of north-west Europe. It often forms up to $30 \%$ of the ostracod fauna, with an average of about $15 \%$. The earliest species so far known is C. nerva Aposto-
lescu. This was originally described from the Sables de Bracheux (Thanetian) of the Paris Basin, but has since been recorded as the subspecies C. nerva montensis Marlière from the Montian of Belgium and Dutch Limburg (Marlière, 1958; Deroo, 1966). C. multicostata Apostolescu is also found in the Sables de Bracheux. Other species are known from the London Clay (Ypresian) of the London and Hampshire


Fig. 3. Suggested lineages of Cytheretta in northwest Europe.
basins (Jones 1956; Haskins, 1968; Eagar, 1965) and from the Sables de Cuise of the Paris Basin (Keij, 1957; Apostolescu, 1964). It is clear that Cytheretta is found near the beginning of the Tertiary, and it is necessary to look into the Cretaceous for its ancestry.

The related genusParacytheretta Triebel ranges from the Senonian to the Palaeocene (Morkhoven, 1963); the type species $P$. reticosa Triebel was described from the Middle Palaeocene of Denmark. Deroo (1966) has described four genera belonging to the subfamily from the Maastrichtian of Dutch Limburg. These include two new genera which are discussed in more detail below. Puri's statement (1958) that Cytheretta stemmed from Paracytheretta late in Palaeocene times therefore needs some modification. It would appear that the genus as now understood probably arose polyphyletically from late Cretaceous forms. Unfortunately Palaeocene and Lower Eocene species are not very well known, nor are Danian relatives, so it is impossible to discuss the origins of Cytheretta in any detail. It is not present in the well studied Maastrichtian faunas, but is in the Montian. The genus probably originated in western Europe, where it is most abundant, but it was already present in the Caribbean region during the Palaeocene (van den Bold, 1957), and also in Greenland (Szcezechura, 197).

Two distinct lineages can be seen amongst the early forms of Cytheretta (Fig. 3). The first is the superspecies C. laticosta (Reuss) which is found throughout the Eocene. The second is the more complicated group which includes $C$. nerva, C. scrobiculoplicata (Jones), C. crassivenia Apostolescu, C. costellata (Roemer), C. bambruggensis Keij, C. decipiens Keij, C. grignonensis Apostoiescu and C. haimeana (Bosquet). The last six of these are Middle Eocene species, although C. crassivenia is also known from the Sables de Cuise (Lower Eocene). It was during Lutetian times that the group underwent a great explosion, both in numbers and in geographical range. Several are found in the Auversian (Sables d'Auvers, Sables de Beauchamp), but apart from C. costellata did not survive into the Bartonian. The Upper Eocene was essentially a period during which the descendants of the Middle Eocene radiation continued to evolve. Compared with the Middle Eocene, the number of species is poor but individuals are abundant. A third group emerged during the Middle Eocene, exemplified by C. eocaenica Keij. The history of this group is fragmentary. Its ancestors are unknown; it is not found in the Upper Eocene of the region, yet in the Lower Oligocene of Aquitaine C. oligocaenica sp. nov. is found which is so close in morphology as to be separable only with difficulty from C. cocaenica. It is possible that this group was ancestral to the Oligocene groups and to the Miocene and Recent species of the Mediterranean.

There were two distinct provinces in the Anglo-Paris region during the Eocene. The London Clay (Ypresian) of the western part of the London Basin has so far yielded only one common member of the genus, $C$. scrobiculoplicata, which is often extremely abundant (Eagar, personal communication). Bowen (1953) records one specimen of the C. laticosta group from Enborne, in the south-west London Basin. No younger species are known, however, because of the unfossiliferous nature of the succeeding strata. The London Clay of the Hampshire Basin also contains C. scrobiculoplicata, together with early members of the superspecies C. laticosta
(Haskins, 1968). For the remainder of the Eocene the superspecies C. laticosta is by far the most abundant Cytheretta. It is joined by C. haimeana, C. costellata, and C. eocaenica during the Middle Eocene, but in the Upper Eocene in most samples examined it is almost the sole representative of the genus. The Paris Basin formed the other province. During the Middle Eocene the C. haimeana group was common, no particular species being predominant; in the Upper Eocene however, C. costellata became completely dominant. In Belgium the picture is not clear, but it is apparently similar to the Paris Basin, although C. eocaenica is by far the commonest species in the Sable de Lède (Ledian).

There was a certain amount of communication between these regions, because C. costellata is occasionally found in the Barton Clay (Bartonian) of the Hampshire Basin, while the superspecies C. laticosta is present in the Paris Basin and Belgium. The communication was much clearer during the Middle Eocene than during the Upper Eocene.

The Oligocene saw an almost complete replacement of the Eocene species. New groups such as the superspecies C. tenuipunctata and C. sagri are dominant. The only groups with known Eocene ancestors are C. rhenana Triebel, C. stigmosa Triebel, and C. oligocaenica. The first two are related to species from the Headon Beds of the Hampshire Basin, C. headonensis Haskins and C. aff. stigmosa Triebel, which in turn are probably related to C. eocaenica. C. oligocaenica is also related to the Middle Eocene $C$. eocaenica. This reflects the general situation amongst the ostracods, i.e. at the base of the Oligocene a completely new fauna is found in western Europe. Provinces existed, as in the Eocene, but with a different constitution owing to palaeogeographical changes. The Paris Basin, Belgium, Mainz Basin, Rhine Graben and Swiss Basins formed one unit, and Aquitaine another. Within these are found sub-provinces due to geographical separation with the attendant evolution of distinct sub-species.

The genus Flexus Neviani is first reported from the Sables de Cuise (Cuisian) of the Paris Basin (Apostolescu, 1964). Cytheretta decipiens was placed in the genus Flexus by Puri (1958), but for reasons given below it is here retained in Cytheretta. However, this was probably the ancestor of $F$. concinnus (Triebel) (Keij, I957; and see below). An undescribed species of Flexus has been observed in the Lutetian (Fisher Bed VII) of Whitecliff Bay, which is thought to have been derived from an early member of the superspecies C. laticosta. The genus is fairly common, though never abundant, in the Upper Eocene; it is represented by $F$. solentensis sp. nov. and $F$. ludensis sp. nov., the origins of which are unknown. In the Oligocene the genus is represented by $F$. concinnus; the type species $F$. plicatus (von Munster) comes from the Chattian. As used here, the genus is undoubtedly polyphyletic.

## IV. EVOLUTION OF MID-TERTIARY CYTHERETTINAE

Various types of evolutionary pattern were exhibited by the Cytherettinae during Tertiary times. The $C$. haimeana species group is a good example of cladogenesis as defined by Sylvester-Bradley (1962). Using his terminology (Fig. 4) it is possible to recognize a first period of stabilization in the Palaeocene and Ypresian. During


Fig. 4. The evolution of the C. haimeana species group.
this lengthy period, gradual evolution (stasigenesis) was taking place whereby C. montensis gave rise to C. nerva, which in turn led to C. scrobiculoplicata. In the Upper Ypresian (=Cuisian) a period of eruption began which continued into the Lutetian. During this period seven new species appeared. Perhaps significantly this coincided with a transgression of the sea, giving large areas of shallow marine waters ideal for Cytheretta, and presumably leading to a reduction in the selection pressure. The Middle Eocene (Lutetian and Auversian) was a time of extreme variation, and by the end of the Auversian most of the species were extinct. The Bartonian saw a second period of stabilization, with two gecgraphical subspecies of C. costellata, and the descendants of C. decipiens which were now almost generically distinct. Flexus s.s. appeared in the Oligocene, representing the last members of the group. Final extinction occurred in the Quaternary. Within the species group the evolution of the subspecies of C. costellata shows a pattern very similar to the classic Zaphrentis delanouei as interpreted by Sylvester-Bradley (195I). In the Lutetian, C. costellata costellata consisted almost entirely of one morphotype; great variation occurred in the Auversian, with seven morphotypes, followed by stabilisation in the Bartonian where the subspecies consist mainly of one morphotype in each geographical region.

As opposed to this pattern, the superspecies C. laticosta shows gradual evolutionary change, without any period of explosive evolution.

A second period of eruption of the Cytherettinae occurred near the base of the Oligocene, once again coinciding with the spread of shallow seas over much of Europe. The superspecies C. tenuipunctata shows great eruption in the Lower Rupelian, with the presence of many geographical subspecies. This was followed by stabilization in the Upper Rupelian and Chattian.

Specific examples of evolution are dealt with in the taxonomic descriptions. These are C. costellata, C. eocaenica, C. laticosta, C. buttensis, C. sagri, and F. solentensis.

## V. ECOLOGICAL DISTRIBUTION OF RECENT SPECIES

Three species are known from the Mediterranean:
C. judaea (Brady) the type species, is described by Kruit (I955) from the marine, shallow water ( $5-\mathrm{I} 5 \mathrm{~m}$ ), sandy deposits of the Rhone delta; Puri, Bonaduce \& Malloy (1965) report it being found in association with Posidonia meadows in shallow banks around the islands and peninsulars of the Gulf of Naples, where the salinity is about $38 \%$ and the bottom water temperature $14-15^{\circ} \mathrm{C}$; Rome records it from the shallow waters at Monaco ( $0-3 \mathrm{~m}$ ) associated with Posidonia; Ascoli (1965) found it in waters up to 74 m deep in the Adriatic Sea. Brady originally recorded it from the coast of Syria.
C. adriatica Ruggieri is apparently more restricted, but no details are available; it is found in beach sands at Rimini associated with C. judaea.
C. belgica (Brady) is reported by Kruit (1955) trom the marine, sandy sediments of the Rhone delta in water of ro- 15 m depth. These specimens may however be identical to C. adriatica.

Three species are present around the coasts of southern North America from the Bahamas, Florida, the Gult coast and New York. These are C. edwardsi (Cushman), C. sahni Puri and C. tracyi Blake. C. sahni is reported by Hulings and Puri (r965) from a sand mud mixture in water less than 65 ft deep and with a salinity greater then $30 \%$. No details are known for the other two.

In the same region two species of Protocytheretta are present:
$P$. daniana Brady is reported by Puri and Hulings (1957) from clastic sediments at depths of $36-65 \mathrm{ft}$, more commonly in the deeper part; salinity, $28-35.6 \%$ o, clear water, temperature between $10^{\circ}$ and $30^{\circ} \mathrm{C}$; it is absent in the carbonate province of Florida. Curtis ( 1960 ) found it in sands, silts, and clays, particularly in water with an estuarine influence but predominantly marine; temperature $24-25^{\circ} \mathrm{C}$. Kornicker (1965) mentions that it is found around the Bahamas.
P. multicarinata Swain was recorded by Swain (1955) from the nearshore Gulf of Mexico.

Cytheretta knysnaensis Benson is recorded by Benson \& Maddocks (1964) from the Knysna estuary, South Africa, where it is found in muddy sands free from wave action but with a fair current; salinity is $28.4 \%, \mathrm{pH} 8$; it is associated with a partly marine and partly estuarine fauna. However, following the description of this species there are reasons for believing it may not be a true Cytheretta; the inner margin, radial pore canals and central muscle scars are different, there is a vestibule and an internal eye sinus, which Cytheretta does not have.

To sum up, Cytheretta is normally found in shallow ( $10-30 \mathrm{~m}$ ) nearshore clear waters of normal salinity; the temperature is warm ('Mediterranean') with a bottom water temperature of about $15^{\circ} \mathrm{C}$; the substratum is a sand or sandy clay, often covered with seaweed. The genus Protocytheretta seems to be able to tolerate slightly brackish conditions with a salinity as low as $28 \%$.

## VI. PALAEOECOLOGY

The genus undoubtedly inhabited a similar environment during the Eocene as the recent species. This accounts for its abundance in the Tertiary of the Paris Basin, London Basin, Hampshire Basin, Belgium, Mainz Basin and the Swiss basins. These were all shallow water areas, except for the eastern part of the London Basin where the genus has not been recorded so far. The clear distinction between the London and Hampshire basins on the one hand and the Paris Basin on the other is probably in part geographical and in part related to the contrast between the sediments of the two regions. In the former the ostracods are mainly found in argillaceous deposits, while they are found in arenaceous and calcareous depositsin the latter.

The Upper Eocene of Biarritz has yielded only one or two specimens of Cytheretta, while Cytherella and Pontocyprella are extremely abundant. On the other hand, some inland exposures contain fairly abundant Cytheretta. The Oligocene of Biarritz also contains abundant Cytheretta. This is undoubtedly ecologically controlled. The Upper Eocene saw deep water at Biarritz which shallowed eastwards, eventually giving way to continental deposits; at the end of the Eocene the water shallowed with a change from argillaceous to arenaceous deposition.

The Headon Beds of the Hampshire Basin contain sediments deposited in a variety of environments ranging from freshwater to shallow marine. Ostracods are found in most of these environments, but Cytheretta is restricted to the marine phases; as soon as brackish conditions prevailed Cytheretta disappeared. Thus it is found in association with such genera as Pterygocythereis, Trachyleberidea, Bradleya, Leguminocythereis, Brachycythere and Haplocytheridea. Whenever such genera as Neocyprideis or Cytheromorpha become abundant, Cytheretta is no longer present.

## VII. GEOGRAPHICAL DISTRIBUTION

Fossil species have so far been reported from the Palaeocene, Eocene, Oligocene, Miocene, Pliocene and Quaternary of Europe; from the Palaeocene, Eocene, Oligocene, and Miocene of North America and from the Palaeocene of Greenland (Szczechura, 197I) ; Latham (1938) recorded Cytheretta costellata (Roemer) from the salt range, Punjab, but this is a misidentification and is probably a species of Buntonia. In space Cytheretta would appear to be restricted to the coasts of the North Atlantic and adjacent seas; the case of the South African C. kysnaensis has already been mentioned. Its greatest development is in Europe, where some hundred species, both fossil and recent, have been described.

Flexus has only been reported from western Europe where it ranges from the Lower Eocene to the Quaternary, the latest recorded species being F. triebeli Ruggieri from the Upper Pliocene and Lower Quaternary of Italy (Ruggieri, 1952).

Protocytheretta is restricted to North America where it ranges from the Oligocene to Recent. It is found in the Gulf of Mexico, and also off the west coast of California and Mexico (Swain, 1969).

Recently described genera are mainly known from their type areas only. Thus Acuticytheretta and Semicytheretta are only known from western Europe, while Bensonia, Grekoffiana, and Argenticytheretta are only recorded from south America. For a discussion of these see the next section.

## VIII. CLASSIFICATION OF THE SUBFAMILY CYTHERETTINAE

Following Hazel (I967) the Cytherettinae are regarded as a subfamily of the Trachyleberididae; this based on the muscle scars, hinge, and soft parts.

The following genera have been included by various authors within the subfamily: Cytheretta Muller, 1894; Flexus Neviani, 1928 (syn. Eucytheretta Puri, 1958) ; Pseudocythereis Skogsberg, 1928; Buntonia Howe, I935; Paracytheretta Triebel, 194I; Loculicytheretta Ruggieri, 1954; Ambocythere Van den Bold, 1957; Protocytheretta Puri, 1958; Netrocytheridea Howe and Laurencich, 1958; Neocytheretta Morkhoven 1963; Acuticytheretta Deroo, 1966; Semicytheretta Deroo, 1966; Bensonia Garcia, 1969; Grekkofiana Garcia, I969; and Argenticytheretta Garcia, Ig69.

Loculicytheretta was placed in the subfamily by both Ruggieri (1954) and Howe (Treatise, 196I), but its distinctive characters would seem to exclude it. Deroo (I966) placed Netrocytheridea into the subfamily; however its shape and entomodont hinge would appear to exclude it. The only real similarity is in the irregular shape
of the inner margin. Ambocythere was included by Morkhoven $(\mathrm{Ig62}, 3$ ) because of its supposed ressemblance to Buntonia; its false radial pore canals, branching radial pore canals, and lateral shape do not support its inclusion. Neocytheretta from Indonesia is not considered to belong to the subfamily. It has eye spots (Cytheretta is blind), a completely different type of ornamentation, and a different hinge; only the irregular inner margin resembles Cytheretta.
Pseudocythereis was placed in the subfamily by Puri; no material has been available for study, only the original description of Skogsberg could be examined. The type species is Cythereis (Psendocythereis) spinifera Skogsberg, and the author was undoubtedly comparing it with C. rubra Müller as far as the soft parts were concerned, but the description of the shell is inadequate. Therefore, no conclusion could be reached concerning it, except to agree with Puri that there are strong resemblances to Cytheretta.
Paracytheretta has a very well developed anterior hinge ear in the left valve and no other Cytheretta species approach it in this respect. The hinge is apparently similar to Cytheretta (Morkhoven, 1963), the surface of the valve is reticulate with three longitudinal ridges.

The development of three longitudinal ridges is a common feature of the subfamily, but not all such forms are necessarily closely genetically related. Puri recognized three such genera, Paracytheretta, Eucytheretta, and Protocytheretta. The latter was said to be Cytheretta-shaped, while the others were Cythereis-shaped; the first two were then differentiated on the hinge, which is Cytheretta-like in Eucytheretta and Cythereis-like in Paracytheretta. However, Triebel's original description of the hinge of Paracytheretta, as shown by Morkhoven (1963) is the same as for Cytheretta. There is, however, no doubt that Paracytheretta is a valid genus because of its distinctive shape. Flexus has a totally different shape, much more like that of Cytheretta. Flexus and Protocytheretta can be separated, both on shape and ornamentation. The only species studied that Puri placed into Protocytheretta is P. schoelleri Keij from the Oligo-Miocene of Aquitaine; apart from this species the genus would be restricted to North America. A study of descriptions and illustrations of $P$. daniana, the type species, suggests that $P$. schoelleri does not belong to the same genus, and therefore, that the genus is probably restricted to North America (see description and discussion in $P$. schoelleri below).
Flexus has already been shown to be polyphyletic. It is used here for all species shaped like the type species, $F$. plicatus (von Munster) and having three prominent longitudinal ridges. This is not a very satisfactory arrangement, but present knowledge makes it very difficult to divide it into new genera.

Similarly, no attempt has been made to further subdivide the genus Cytheretta. As mentioned above, there are six distinct groups in the Eocene and Lower Oligocene of western Europe. However, the recognition of such monophyletic groups is difficult to correlate with easily diagnosed morphological characteristics, so it has been thought better for the present to limit their taxonomic recognition to the rank of superspecies. Further investigation, particularly of Lower Tertiary forms, should lead to a phylogenetic division of the genus; this must be combined with a study of the American species, and so is beyond the scope of the present work.

The six groups mentioned above are:
C. haimeana group
C. laticosta group
C. eocaenica group
C. tenuipunctata group
C. sagri group
C. rhenana group

Acuticytheretta certainly has a Cytheretta-like appearance in general outline, has unequal valves and similar muscle scars to Cytheretta. The inner margin is very wide posteriorly, but not irregular; and the hinge is simpler, with a large anterior tooth in the right valve, and a small anterior tooth at the end of the smooth (?) bar of the left valve, and a posterior tooth in the right valve. It could represent a primitive member of the subfamily.

Semicytheretta has a similar hinge and muscle scars to Cytheretta, but has a narrow and regular inner margin and a different shape.

Deroo also describes Cythere euglypha Bosquet and Cythereis euglyphoidea Van Veen, which from the illustrations could also be included in the subfamily. Their shape, unequal valves, muscle scars, and ornamentation suggest this; the hinge has faintly crenulate anterior and posterior teeth in the right valve, and the inner margin is narrow and regular. They are placed in the genus Anticythereis Van den Bold. These could be early primitive members of the subfamily.

Morkhoven $(1962,3)$ included Buntonia in the subfamily because the first thoracic legs of the male are similar to those of Cytheretta. In general appearance certain Buntonia species can be confused with cytherettinids, although there are noticeable differences in the hinge and the inner margin. It is provisionally included within the subfamily.

Grekoffiana is described as being similar to Protocytheretta, but with a regular inner margin. The type species is G. australis Rossi de Garcia. In the discussion of the new genus (1969; 218), de Garcia placed Protocytheretta daniana (Brady) Benson and Coleman in Grekoffiana. This might be taken to imply the species as interpreted by Benson and Coleman, and not Brady's species; on page 220 we have mention of 'Grekoffiana daniana (Brady) dans Benson et Coleman (1963) (p. 26, Tab. 5, Figs 5, 7, $9 \&$ Io)'; again, perhaps implying the species as interpreted by Benson and Coleman, but in this case there should have been some statement to this effect. The idea is thus given that Brady's species is being included in the new genus, even though it is in fact the type species of Protocytheretta. P. daniana is generally thought of as having a typical cytherettinid sinuous inner margin, although following Benson and Coleman it may in fact show considerable variation. Thus two problems arise: firstly, if $P$. daniana can have a regular or a sinuous inner margin, i.e., it is an infraspecific character, it can hardly be used to diagnose a new genus; and secondly, the type species of a genus cannot be included in a new genus. There are grounds then for wondering whether Grekoffiana is in fact a valid genus, and not a synonym of Protocytheretta.

Bensonia is described as being similar to Cytheretta, but with a regular inner margin. The hinge and overall appearance certainly look like a typical cytheret-
tinid. Cytheretta knysnaensis is placed in this genus, and as stated previously, there are certain features, particularly the implied presence of an eye, which would exclude it from Cytheretta. The presence or absence of any occular structures cannot be determined from Rossi de Garcia's description, so it is difficult to know whether Bensonia is a true cytherettinid genus. It is provisionally placed in the subfamily.

Argenticytheretta is illustrated with what appears to be an eye tubercle, and in overall shape does not resemble Cytheretta. It also has a regular inner margin.

From this it would seem that there exists a group of Cytheretta-like ostracods, principally occurring on the two sides of the south Atlantic, but which differ from true cytherettinids in several respects. Perhaps it is a case of homeomorphy? Until more species are described in detail, this question must remain unanswered.

The genera included within the subfamily are:

|  | Cytheretta |
| ---: | :--- |
|  | Flexus (syn. Eucytheretta) |
| Paracytheretta |  |
| Protocytheretta (syn. Grekoffiana?) |  |
| Acuticytheretta |  |
| Semicytheretta |  |
| Provisionally: | Buntonia |
| Pseudocythereis |  |
| Doubtfully: | Bensonia |
|  | Argenticytheretta |

The characters taken to be diagnostic of the Cytherettinae are: inequivalve, the left valve being markedly larger and differently shaped than the right; a modified holamphidont hinge; presence of a fulcral point; numerous and simple radial pore canals; generally sinuous inner margin; unornamented, or with a predominantly longitudinal ornamentation; development of few posterior spines and many anterior denticles; lack of occular structures, lateral spines, and caudal process.

## IX. THE SHELL STRUCTURE OF CYTHERETTA

Cytheretta typically has an elongate-ovate shape. The dorsal margin is straight to convex, often with a posterior hinge ear and sometimes with an anterior hinge ear in the left valve. The posterior margin is obliquely curved with a sharp, high postero-dorsal angle and a gentle slope round to the ventral margin. The latter is often concave, always so in the right valve. The valves are usually very unequal in size and shape, the left valve being much larger and with a greater height; in lateral view the outline of the left valve over-reaches that of the right valve in most places. This over-reach is particularly prominent in the postero-dorsal angle where the hinge ear is developed and in the anter-dorsal angle where the antero-dorsal lobe (see below) of the hinge of the left valve rests on the antero-dorsal platform of the right. The shape in dorsal view varies. Sexual dimorphism is distinct, the males being more elongate.

The carapace may be completely unornamented, as in the type species. More usual, however, is an elongate ornamentation which can take the form of either
longitudinal rows of pits, usually better developed towards the posterior, or longitudinal ridges. The latter often have reticulation developed between them, and some ridges converge to form a sub-central plexus (Fig. 5). For descriptive purposes the ridges are numbered from the dorsal margin in a position just to the posterior of the sub-central plexus (Fig. 5). The anterior and antero-dorsal regions of both valves are often smooth, while the rest of the carapace is ornamented. The ornamentation is generally similar for both valves.

The hinge is modified holamphidont with several accessory elements (Fig. 6, 7; Plates $5,7,8$ ). In the left valve there is an anterodorsal lobe, which is an outgrowth of the selvage and rests on to an antero-dorsal platform in the right valve. The anterior socket is partially opened ventrally; it is bordered by an antero-ventral lobe which fits into the modified anterior part of the anterior tooth of the right valve, the antero-ventral sinus, which is a hollow in the tooth. The antero-median tooth


Fig. 5. C. costellata (Roemer), showing the system of numbering the ridges. $\times 75$.
is generally small, the postero-median bar is crenulate and swollen at the posterior to give a postero-median swelling. This is sometimes almost as prominent as the antero-median tooth, as in the type species; it forms one edge of the posterior socket, which is almost open ventrally. The posterior socket often forms a posterior hinge ear, sometimes with a lobe. In the right valve the anterior tooth has an almost vertical face towards the anterior; it is sometimes stirpate (=stepped), or with a gentle posterior slope. In lateral view the tooth has a concavity in the anteroventral position, the antero-ventral sulcus. The antero-median socket is shallow, the postero-median groove is crenulate, and there is usually a shallow posteromedian socket. The posterior tooth is generally pessular (i.e. with more or less parallel sides) and is sometimes almost as prominent as the anterior tooth, as in the type species.

There is considerable variation in the details of the duplicature. The selvage is generally more prominent in the right valve. At the anterior it usually has a position close to the outer margin, but in some species it is further away so that a prominent flange groove is formed; there is a wide flange groove developed along the ventral margin of the right valve, with a narrow one along the posterior. The selvage is


Fig. 6. Internal structure of the left valve of Cytheretta.


## Right Valve

Fig. 7. Internal structure of the right valve of Cythevetta.
sometimes very strongly developed at the posterior. The flange usually forms the outer margin. A weak list is often present.

The outline of the inner margin is a characteristic feature; it is broad with three principal indentations (Fig. 7) ; its outline can be divided into three segments for descriptive purposes. It ends against the anterior and posterior hinge elements. The anterior and ventral radial pore canals are long, simple, often crossing one another, usually bulbous near the outer margin (Pl. r). The anterior pore canals tend to be concentrated around the antero-ventral angle. The posterior radial pore canals are rather different (Pl. I, Fig. 9) ; the inner lamella in which they are situated is not fused to the outer lamella, so that a vestibule is in fact formed. The posterior radial pore canals are numerous, straight and very closely packed; often they form two groups, a ventral one of short pore canals similar to the anterior and ventral radial pore canals, and a dorsal one of closely packed pore canals.

The central group of muscle scars consists of a row of four adductors; the lower two often touch and the third one often elongate; and a large irregularly ' U '-shaped frontal scar with a smaller scar in front. A fulcral point is prominent, forming a raised boss; this feature is also a well known characteristic of the Cytherideinae (von Morkhoven, 1963). A dorsal group of about three muscle scars can be detected. There are two mandibular scars which almost touch, or one elongate scar near, and just anterior to, the ventral indentation (Pl. I, Fig. 7).

There is no eye spot or occular sinus, as Cytheretta is blind. The feature often described as an eye spot is the antero-dorsal lobe of the hinge of the left valve.

## X. SOFT PARTS

The soft parts have not been examined during this study, and the only published descriptions are for C. mbra, C. edwardsi (Cushman) I906 and C. tracyi Blake, I929 (Hazel, 1967). The principal characters 'are the three-jointed exopodite of the second antennae, absence of a seta on the posterior border of the protopodite of the first thoracic legs' (Hazel, 1967; 40, after Müller, 1894) and an asymmetry of the first pair of thoracic legs in the male which is developed to varying degrees.

## XI. LARVAL STAGES

Only the last three larval stages have so far been recognized. They tend to be more triangular in shape, with a pointed posterior. Ornamentation in the last moult is similar to that of the adult, but in earlier moult stages is only partially developed. The hinge is very simple; in the left valve the antero-dorsal lobe is developed, followed by an anterior socket open ventrally, smooth bar and posterior socket, also opened ventrally; the corresponding features are present in the right valve.

About one in fifty of the adult specimens appears to be weakly calcified. The hinge is an adult hinge, but weak; the inner margin is straight, without the normal indentations, and very narrow. Pokorny (1965) suggested that such a feature might be due to a parasitic infection and Morkhoven (1963) that the animal died soon after moulting and before calcification was complete. Oertli (1965) mentions the case of

Faluma where the true adult form is very rare, and the thinly calcified moult stage was probably mature, i.e. a case of neotony. Sandberg (1965) supported this by citing cases where such immature forms contained eggs. However, in the case of Cytheretta Morkhoven's explanation is probably the correct one.

In two species, C. cocaenica and C. oligocaenica, a few very large specimens are found. They are about double the size of the normal adult, but otherwise identical. This is a fairly frequent phenomenon in several families of the Ostracoda. Benson (I965) suggests that such forms might be a gerontic stage; and Kesling in the Treatise (rg6r) considers that they represent post-maturation instars.

## XII. THE SHELL STRUCTURE OF FLEXUS

Internal details are the same as for Cytheretta. As defined here, all Cytheretta-like forms with three prominent longitudinal ridges are referred to this genus.

## XIII. THE TYPE SPECIES OF CYTHERETTA

Müller described Cytheretta in 1894 with C. rubra Müller as type species. In 1950 Ruggieri put C. rubra into the synonymy of C. subradiosa (Roemer), originally described from the Pliocene of Italy. This was accepted by Triebel (1952), Puri (1958) and Hazel (1967), but queried by Morkhoven (r963). Thanks to Prof. Ruggieri, who kindly supplied the material, it has been possible to study both forms. Morkhoven also mentioned that C. rubra might be a synonym of Ilyobates? judaea Brady, 1868; Hazel accepted this view, but places both C. mubra and C. judaea within the synonymy of $C$. subradiosa. Fortunately Brady's material is preserved in the collections of the Hancock Museum, No. B67, presently under the care of Dr. K. McKenzie. There is no doubt that C.judaea is the senior synonym. The problem now is whether this is synonymous with $C$. subradiosa.
C. subradiosa was described from the Pliocene of northern Italy at Castellarquato; none of Roemer's material is available for study, but Ruggieri has obtained topotype material. The specimens described below come from the Pliocene of San Arcangelo, near Rimini. Müller's specimens were from the Gulf of Naples; the specimens described below come from the beach sand at Rimini.

A comparison of the Pliocene specimens with the recent has shown a number of differences which are believed to distinguish C. judaea from C. subradiosa. The position of the Quaternary forms is unknown.

The major difference is in the line of the inner margin, particularly the posterior segment. In C. judaea this cannot be separated from the median segment, but in C. subradiosa it is steep, giving a narrow and deep posterior indentation ; the posterior indentation in $C$. judaea is very broad. There are more radial pore canals in C. subradiosa, 32 compared with 24 in C. judaea. The central muscle scars are situated more to the dorsal in $C$. subradiosa; the four adductors are larger and the frontal is more dorsally situated in respect to the adductors. There is a slight difference in shape in that $C$. judaea is more obliquely rounded in the anterior margin. The hinge is almost identical although the anterior tooth of the right valve is slightly more prominent in C. judaea.

Finally, Müller included two distinct species in his description of C. rubra (see below). One is probably synonymous with C. judaea and the other with Cytheridea striatopunctata Terquem 1878.

## XIV. SYSTEMATIC DESCRIPTIONS

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily CYTHERETTINAE Triebel, 1952
Genus CYTHERETTA Müller, 1894
1894 Cytheretta Müller, p. 382
1906 Pseudocytheretta Cushman, p. 382
1928 Cylindrus Neviani, p. 106
1941 Prionocytheretta Mehes, p. 60
Diagnosis: The carapace is elongate-ovate, with a gently curving postero-ventral angle so that the posterior margin is markedly asymmetrical. Generally very inequivalve, with a large left valve. Ornamentation consists of longitudinal ridges or rows of pits, or the carapace may be smooth. The hinge is modified holamphidont. The line of inner margin is sinuous; the duplicature is wide; selvage, flange, and list are developed to varying extents; the radial pore canals are simple, long, bulbous, and curved; the normal pore canals are simple. The central muscle scars consist of a row of four adductors and a large irregularly ' U '-shaped frontal; a fulcral point is well developed.

Type species: Ilyobates? judaea Brady.
Discussion: The type species of Cylindrus is C. jurinei (von Munster) which is a true Cytheretta; the name Cylindrus is also preoccupied (Fitzinger, 1833, Mollusca). Neither of the other two have been studied; Puri (1958) states that the shell structure of Pseudocytheretta is identical with that of Cytheretta, and Hazel (1967) discusses the genus in some detail and concludes that it is synonymous with Cytheretta. Triebel (1952) places Prionocytheretta in the synonymy of Cytheretta.

## Cytheretta judaea (Brady)

(Pl. I, fig. I, 4-7, 9; Text Fig. 8)
1868 Ilyobates? judaea Brady: 112, pl. 13, figs $17,18$.
1894 Cytheretta rubra Müller: 382, pl. 8, figs. 9, 10, 16; pl. 39, figs 8-22, 24.
1912 Cytheretta rubra Müller; Müller: 366.
1950 Cytheretta subvadiosa (non. Roemer; pars); Ruggieri: 9.
1953 Cytheretta subvadiosa (non. Roemer; pars); Ruggieri: 102.
1955 Cytheretta rubra Müller; Kruit: 482, pl. 5, figs 9a-c.
1958 Cytheretta subradiosa (non. Roemer; pars); Puri: 186, pl. 1, figs 3-7.
1959 Cytheretta subvadiosa (non. Roemer; pars); Ruggieri: 190.
Diagnosis: A species of Cytheretta with sub-parallel dorsal and ventral margins and unornamented surface. The inner margin is almost straight.

Material: Thirteen valves and carapaces from the beach sand at Rimini; Io 3792-4; 3810.
Type locality and horizon: Haifa, Recent.
Stratigraphical Range and distribution: Recent-Rhone delta, Monaco, Naples, Adriatic Sea, Syria, Aegean Sea; Quaternary of Italy?

Description: Sexual dimorphism is not strong; the males are more elongate. Sex ratio $1 \cdot 5$. The left valve has a weak posterior hinge ear; the dorsal margin is slightly convex; the anterior margin is strongly obliquely rounded. The ventral margin is almost straight and roughly parallel to the dorsal margin; the posterior margin is obliquely rounded. The greatest height is just to the posterior of centre. The ventral margin of the right valve is concave. In dorsal view the carapace is ovate, tapered towards the anterior.

The shell is smooth, but with conspicuous opaque areas; there is a large one in the central region and a smaller one in the anterior. These are approximately constant in position in all specimens, producing the black areas seen in Pl. I, fig. 4.

The antero-dorsal lobe of the hinge of the left valve is flat; the postero-median swelling is pronounced. In the right valve the posterior tooth is almost equal in prominence to the anterior tooth.


Fig. 8. Cytheretta judaea (Brady); left valve; $\times 75$.

The anterior indentation of the inner margin is wide and downward pointing; the anterior segment is gently curved; the median and posterior segments cannot be separated; the posterior segment is large and broadly rounded. There are some 24 anterior, 27 ventral, and 32 posterior radial pore canals. The posterior set can be divided into two groups; a ventral group of ten, widely spaced and bulbous, and a dorsal group of 22 , very close together and straight. There are some 25 scattered normal pore canals. The selvage is close to the outer margin, with a flange groove along the ventral margin.

Dimensions:

|  | Left valve |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | $\mathrm{L} / \mathrm{H}$ | L | H | $\mathrm{L} / \mathrm{H}$ | Carapace |
| Female | 0.75 | 0.43 | I .74 | 0.75 | 0.40 | I .88 | 0.42 |
| Male | 0.79 | 0.43 | I .84 | 0.78 | 0.39 | 2.00 | 0.40 |

Discussion: Müller (pl. 8, fig. 13) and Puri (pl. I, figs 9-13) illustrate large specimens with longitudinal rows of puncta. These must represent a different species; as well as the differences already mentioned, the anterior margin is much squarer than the obliquely rounded C. judaea. Triebel ( $1952 ; 17$ ) suggests that these belong to Cytheridea striatopunctata Terquem, described by Terquem (1878) from the Pliocene of Rhodes. Several specimens of this type were found in the sample from Rimini, and were first thought to belong to C. adriatica Ruggieri; however, none have such strong longitudinal ridges as those illustrated by Puri (1958, pl. 2, figs 1-5). They are perhaps members of a gradational series in which C. adriatica represents the morphotype with the strongest developed ornamentation.

See also the generic discussion (p. 281).

## Cytheretta subradiosa (Roemer)

(Pl. I, fig. 8)
1838 Cytherina subvadiosa Roemer: ${ }^{517}$, pl. vi, fig. 20.
1880 Cytherella calabra Seguenza: 326, 366, pl. 17, fig. 56.
1900 Cytheridea subradiosa (Roemer); Namias: 105, pl. 15, fig. 17.
1905 Bairdia subradiosa (Roemer); Cappelli: 306, pl. 9, fig. 4.
1928a Cytheridea subradiosa (Roemer); Neviani : 66.
1928b Cytheridea subradiosa (Roemer); Neviani: I3I.
1950 Cytheretta subradiosa (Roemer); Ruggieri; 9-II (pars).
1953 Cytheretta subvadiosa (Roemer); Ruggieri: 102 (pars)
1959 Cytheretta subradiosa (Roemer); Ruggieri: 190 (pars).
Diagnosis: An unornamented species of Cytheretta with sub-parallel dorsal and ventral margins. The inner margin has a steep posterior segment.

Material: Five carapaces and valves, together with several fragments, from the Lower Pliocene of San Arcangelo, near Rimini. Io 3795.

Type locality and horizon: Castellarquato; Pliocene.
Stratigraphical range and distribution: Pliocene of Sicily, Calabria, Castellarquato, and Rimini; Quaternary of Italy?

Description : The left valve has a very weak posterior hinge ear; the dorsal margin is almost straight, although in some specimens there is a distinct convexity in the central region which interrupts the smoothness of the margin. The anterior margin is obliquely rounded. The ventral margin is straight in the presumed females, but concave in the one specimen thought to be a male. The posterior margin is broadly rounded. The right valve has a greater height towards the posterior; the ventral margin is concave. The carapace is ovate in dorsal view.

The shell is smooth, with no ornamentation.
The hinge of the left valve has a flat antero-dorsal lobe; the antero-ventral lobe is weak; the postero-median swelling is pronounced and equal in size to the anteromedian tooth. In the right valve the posterior and anterior teeth are equal in size.

The anterior indentation of the inner margin is wide and downward pointing; the ventral indentation has a flat base instead of the usual ' $V$ ' shape; the posterior indentation is narrow, deep and curved. The anterior segment is almost straight; the median segment is slightly irregular, with a gentle upward slope towards the posterior; the posterior segment is very steep. There are some 32 anterior, 34 ventral, and 32 posterior radial pore canals; and 25 scattered normal pore canals. The selvage runs very close to the margin; there is a small flange groove along the ventral margin.

Dimensions: Carapace

|  | L | H | W | L/H |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.75 | 0.45 | 0.37 | I .67 |
| Male | 0.8 I | 0.44 | 0.36 | I .84 |

Discussion : From the few specimens studied, there would appear to be considerable variation in shape. See also the generic discussion (p. 28r).

## Cytheretta costellata (Roemer)

Diagnosis: A species of Cytheretta with a characteristic ornamentation of ten longitudinal ridges which unite and bifurcate in a regular pattern; posterior margin with four strong spines, anterior margin with some nine denticles. Strongly inequivalve. Duplicature with an anterior flange groove and a ventral list.

Description: Seven morphotypes have been recognized, chiefly on ornamentation. These are described below.

The ornamentation consists of ten longitudinal ridges with varying ornamentation between (see Text-fig. 5). The second ridge bifurcates towards the posterior and the lower part eventually joins ridge no. 3 ; from the junction a thin ridge runs into no. 4 . Ridge no. 4 is prominent, and forms the dorsal limit to the subcentral plexus towards the anterior. No. 5 forms the ventral limit and again is prominent; in the posterior of the valve it joins no. 7. No. 6 appears to be enclosed between 5 and 7, and joins one of these two. No. 7 is very prominent and extends further towards the posterior than any other; 8 and 9 join together in a position level with the sub-central plexus, 9 bifurcating just to the posterior. An area of reticulation of varying size is present at the anterior.

The antero-dorsal lobe of the hinge of the left valve is swollen; the antero-ventral lobe is poorly developed; the antero-median tooth is prominent and downward pointing; the postero-median swelling is pronounced but small in comparison with the antero-median tooth; the posterior socket is circular rather than ovate.

There are some 30 anterior pore canals, about 30 very closely packed posterior radial pore canals, and 15 ventral radial pore canals. The selvage is prominent; a flange groove is present, particularly prominent in the right valve, both anterior and posterior. Four spines come from the flange at the posterior and some 9 denticles are developed along an anterior fringe. A faint list is developed, particularly along the ventral side.

The central muscle scars are in a slight pit ; they are small, the two ventral scars close together, the third elongate, and the dorsal-most scar circular.

Sexual dimorphism is pronounced; sex ratio $1 \cdot 75$.
Discussion (I): Roemer ( I 838 ) originally described the species from the Tertiary of the Paris Basin; the specimen illustrated has six ridges and four or five posterior spines. Its shape is similar to the Lutetian forms of the species to be described below. Bosquet (1852) recorded it from the Sables infèrieurs, Calcaire grossier, and the sables moyens; it was commonest in the Calcaire grossier. His diagram shows eight ridges and four spines. Keij (1957) redetermined Bosquet's material and records several species and genera amongst it. Roemer's material is thought to be lost and Keij's revision of Bosquet's material has been followed in the interpretation of the species. There is, therefore, still some doubt about the identity of Roemer's

| LOCALITY | MORPHOTYPES |  |  |  |  |  |  | SUBSPECIES |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | A | 8 | C | D | E | F | G |  |
| BARTON (7) | - | - | - | - | - | 14.3 | 85.7 | antecalva |
| CHAVENCON (109) | - | - | - | - | - | 100 | - | cratis |
| VERZY (162) | - | - | - | - | - | 100 | - |  |
| LE RUEL (7) | - | - | - | 28.6 | 42.9 | 14.3 | 143 | grandipora |
| MOISELLES (52) | 15.4 | 19 | 7.7 | 15.4 | 59.6 | - | - |  |
| AUVERS (20) | 45.0 | 15.0 | 5.0 | 15.0 | 20.0 | - | - |  |
| BRACKLESHAM (97) | 100 | - | - | - | - | - | - | costellata |
| DAMERY (61) | 100 | - | - | - | - | - | - |  |

Fig. 9. Morphotypes and subspecies of C. costellata (Roemer).
The numbers in brackets refer to the number of specimens examined.
species. Bosquet (1852) mentions Roemer in his acknowledgments for supplying material however. Jones and Sherborn's new variety C. costellata var. triangulata from the type Bracklesham Beds is a female dimorph.

Amongst the material studied it is possible to recognize seven morphotypes which fall into four groupings, here recognized as subspecies. Three of these are chronological subspecies and the fourth is geographical. (Text-fig. 9). For a discussion of the subspecies as used here see Sylvester-Bradley i95r.

## Morphotype A:

The left valve, particularly of the female, is triangular with its apex at the anterior; the dorsal margin is gently convex with a prominent posterior hinge ear; the ventral margin is slightly convex, sweeping round at the posterior in a continuous curve to form the ventral part of the posterior margin; the dorsal part of the posterior margin turns sharply round to meet the hinge ear. The anterior margin is obliquely rounded. The right valve is much lower than the left with a strongly convex dorsal margin and a concave ventral margin. In dorsal view the carapace is ovate.
The ornamentation between the ridges consists of a fine punctation. In the anterior part of the valve the ridges tend to become submerged within a large area of reticulation. A strong marginal rim runs around the anterior and dorsal margins. The sub-central plexus is simple. Ridge no. 6 is joined at both ends to no. 7 by a fine thread-like continuation.

The outline of the inner margin differs slightly between the two valves. The anterior indentation is small and pointed; the anterior segment slopes down quite steeply to the small and ill-defined ventral indentation. In the left valve the median segment is at first level and then slopes upwards to the posterior segment, where the slope steepens markedly and sweeps up close to the dorsal margin; then it curves sharply downwards to form a deep and narrow posterior indentation. In the right valve the median segment is entirely level. In the males the posterior segment reaches much closer to the ventral margin.

## Morphotype B:

Similar in most respects to Morphotype A. However, a very strong and characteristic sub-central plexus is developed, especially well seen in a specimen from Bambrugge (Pl. 2, fig. 5). It consists of a raised platform between ridges 4 and 5 with three pits on its surface. This is a character developed in all the remaining morphotypes and is generally very prominent. The shape is slightly different to Morphotype A as the ventral margin is more convex and so the carapace appears to be much less triangular.

Morphotype C:
The shape of this and the remaining morphotypes is similar to that of Morphotype $B$ but with the development of an anterior hinge ear in the left valve.

The ornamentation between the ridges consists of a punctation intermediate in size between that of Morphotype A and that of Morphotype F. This and the
remaining morphotypes show a slight difference in ornamentation between the two valves. In the left valve ridge no. 6 , joins No. 7 in the anterior but ends without joining either 5 or 7 at the posterior; in the right valve of some specimens ridge no. 7 bifurcates near the posterior margin, the dorsal branch is joined by no. 5 and the ventral branch joins no. 8. There is a prominent sub-central plexus. The anterior area of reticulation is much reduced compared with Morphotypes A and B.

## Morphotype D:

Large pits are developed between the longitudinal ridges, but can only be seen by straining. The pits are not developed in the posterior regions and cover a larger area of the valve in some specimens than in others. Other features are similar to Morphotype E.

## Morphotype E:

This has a strong development of large pits between the ridges. The large pits are two abreast between the median portions of ridges no. 3 and 4 , and in this respect Morphotype E differs from Morphotype F, which has a network of small pits. Ridges 5 and 7 join in the posterior, leaving an unattached no. 6 between them. The anterior area of reticulation is smaller than in Morphotype A, but larger than in Morphotype F.

## Morphotype F:

The anterior margin is evenly rounded and in this respect differs from Morphotypes A-E. Pitting is developed between the ridges; the pits are large between ridges $3-7$, but form a network of small pits between 1,2 , and 3 . The anterior area of reticulation is narrow, only two reticules wide; this results in the longitudinal ridges being more prominent in the anterior region than in Morphotypes A-E. The subcentral plexus is prominent. In the left valve ridge no. 5 is the strongest at the posterior and 6 and 7 join it; a few examples can be seen where no. 5 joins no. 7 , and a few in which the ridges do not join at all. In the right valve no. 7 bifurcates near the posterior, the dorsal portion usually joining 5 and the ventral portion joining 8. This pattern is also present in a few left valves.

The inner margin differs from that of Morphotypes A-E; the posterior segment is not so steep and does not reach so far towards the dorsal margin; the posterior indentation is therefore not so deep.

## Morphotype G:

This is similar to Morphotype F except for the development of a smooth area at the anterior. This varies in extent; in some specimens it is small, in others it extends almost to the sub-central plexus. Both males and females are affected. In the left valve ridge no. 5 is the most prominent at the posterior; no. 6 joins 5 or 7 or neither. The right valve is similar to that of Morphotype F.

## Cytheretta costellata costellata (Roemer)

(Pl. 2, fig. I-IO)

1838 Cytherina costellata Roemer: ${ }^{1} 7$, pl. 6, fig. 24.
1852 Cythere costellata (Roemer); Bosquet: 58 (pars), pl. 2, fig. ix.
1857 Cythere costellata (Roemer); Jones: 32, pl. 5, fig. Ix.
1874 Cythere costellata (Roemer) ; Brady, Crosskey and Robertson: 152, pl. 16, figs 13-15.
1889 Cythere costellata (Roemer) var. triangulata Jones and Sherborn: 30, pl. 1, fig. 21.
1955 Cytheretta costellata (Roemer); Apostolescu: 26, pl. 5, figs 75, 76.
1957 Cytheretta costellata (Roemer); Keij: 132, pl. 22, fig. 7.
Diagnosis: A subspecies of $C$. costellata with fine puncta between the ridges and usually with a simple sub-central plexus.

Material: Material was examined from the following localities; Lutetian IV of Damery, Fisher Beds 2I-24 of Selsey, the Keij Collection at Utrecht (Belgian Lutetian and Ledian), Ledian of Bambrugge. For numbers see Text-fig. 9. Io 3796-3803.

Type locality and horizon: Lutetian of the Paris Basin.
Stratigraphical range and distribution: See Text-fig. io.
Description: This is composed of Morphotypes A, B, and C. It is small in size (see Text-fig. II and Discussion II).

Remarks: The Ledian specimens at Utrecht have not been included in Text-fig. 9 because these were only measured and not divided into morphotypes. Most of them are Morphotype A; a few show very faint pitting in places and are therefore Morphotype D. The specimens mentioned by Keij (1957; 133) as being reticulate are not C. costellata.

## Cytheretta costellata grandipora subsp. nov.

## (Pl. 3, figs I-8)

1852 Cythere costellata; Bosquet: 58 (pars).
1957 Cytheretta costellata (Roemer); Keij: 132 (pars), pl. 6, fig. 9.
Derivation of name: Latin-grandis, large, and pora, pit; refers to the large pits developed between the ridges.

Diagnosis: A subspecies of $C$. costellata characterized by the presence of large pits between the longitudinal ridges with a well developed sub-central plexus.

Holotype: Io 3804 , a female left valve.
Paratypes: Io $3805,3806,3808-9,38$ it-i3.
Material: See Text-fig. 9 .
Type locality and horizon: Carrière de Moiselles, Sables de Beauchamp.
Stratigraphical range and distribution: Sables d'Auvers, Auvers-sur-Oise; Sables de Beauchamp, Moiselles; Sables de Cresnes, Le Ruel. All are in the Paris Basin.

Description: This consists of Morphotypes A-G, but principally A-E; thus there is a great range in ornamentation and size. For size, see Text-figs 9 and Io.

Cytheretta costellata cratis subsp. nov.
(Pl. 4, figs $\mathrm{I}-8$; Pl. 5, figs I-3. Text-fig. 5)
Derivation of name: Latin-cratis, wickerwork; refers to the ornamentation.
Diagnosis: A subspecies of $C$. costellata characterized by the development of pits between the ridges and a narrow area of reticulation at the anterior.

Holotype: Io 38i4, a female left valve.
Paratypes: Io 3815-3822.
Material: See Text-fig. 9.
Type locality and horizon: Verzy; Marnes à P. ludensis.
Stratigraphical range and distribution: Marnes à $P$. ludensis of Verzy and Chavençon in the Paris Basin.

Description : This consists entirely of Morphotype F. For dimensions see Textfig. II.

ENGLAND
PARIS BASIN
BELGIUM


Fig. Io. Stratigraphical and geographical distribution of the subspecies of Costellata (Roemer).

Cytheretta costellata antecalva subsp. nov.
(Pl. 4, figs 9-II)

1968 Cytheretta costellata (Roemer); Haskins: 165; Pl. 2, fig. 1-8.
Derivation of name: Latin-ante, anterior, and calvus, smooth; refers to the smooth anterior region.
Diagnosis: A subspecies of $C$. costellata characterized by a smooth area at the anterior; pits are present between the longitudinal ridges.

Holotype: Io 3823 , a female left valve.
Paratypes: Io 3824-6.


Fig. ri. Size distribution of $C$. costellata (Roemer). PVY=Verzy; $P C C=$ Chavencon; PMS $=$ Moiselles.

Type locality and horizon: Barton; Upper Barton Beds, Bed H (Chama Bed).
Stratigraphical range and distribution: Middle and Upper Barton Beds, Barton; Middle Barton Beds, Alum Bay.

Description: This consists of Morphotypes F and G, but mainly the latter.
Dimensions: Holotype, $\mathrm{L}=0.77 \mathrm{~mm}$.
Remarks: Although the number of specimens is small, a further set of specimens was described by Haskins (1968) from Alum Bay which also had a smooth anterior region, so that this is apparently a well marked character.

Discussion (II): Each assemblage studied shows a range of variation, indicated rather crudely by the proportion of morphotypes it contains. In fact gradations between morphotypes occur and the division into discrete groups is therefore arbitrary. The differences between subspecies are marked by changes in the proportion of the constituent morphotypes. Most of these changes can be correlated with stratigraphical position, but in the case of $C$. costellata cratis subsp. nov. and C. costellata antecalva subsp. nov. it seems probable that we are dealing with contemporary subspecies that are geographically separated. The suggested relationships between the subspecies of $C$. costellata are shown in Text-fig. Io.

In general there is an increase in size with time. This is clearly seen in Text-figs II \& I2. A comparison between the morphotypes found at Auvers and Moiselles (Text-fig. I2) shows that Morphotype A tends to be the smallest and E the largest.


Fig. 12. Size distribution of morphotypes of C. costellata (Roemer) from Auvers-sur-Oise.

This is much clearer in the case of the females than the males. The species from Verzy are smaller than those from Chavençon; as these are of the same age, and because most other ostracods are similarly affected, this is thought to be ecologically controlled. The specimens from the Belgian Sable de Lède are much larger than those from Damery and Bracklesham.

The ridge pattern remains remarkably constant, apart from the posterior involvement between ridges nos. 5, 6 and 7. With time there is an increase in complication of the ornamentation between the ridges and a decrease in the width of the anterior area of reticulation. At the posterior ridge no. 7 is at first the most prominent and no. 5 and 6 join it; this changes until no. 5 is the strongest and no. 6 and 7 join it (Text-fig. I3).

The anterior margin changes from obliquely rounded to evenly rounded. The Ludian forms are proportionally higher than the Lutetian ones.


Fig. 13. Changes in ridges 5,6 and 7 of C. costellata (Roemer).

## Cytheretta bambruggensis Keij

(Pl. 3, fig. 9)

1957 Cytheretta bambruggensis Keij: 131, pl. 6, fig. 10, pl. 10, figs 9-11.
Material: One right valve from the Sables de Lède of Bambrugge. Io 3827 .
Type locality and horizon: Bambrugge (Belgium); Sables de Lède.
Stratigraphical range and distribution: Lutetian, Ledian and basal Sables de Wemmel, Belgium; 'Bartonian' of the borehole at Delden, the Netherlands.

## Cytheretta crassivenia Apostolescu

$$
\text { (Pl. 6, figs } 2,5 \text { ) }
$$

1852 Cythere costellata (non Roemer; pars); Bosquet: 58.
1955 Cytheretta crassivenia Apostolescu: 261, pl. 5, figs 77-79.
1957 Cytheretta crassivenia Apostolescu; Keij: pl. 6, fig. 4; pl. 10, figs 12-14.
Material: Two valves from the Lutetian of Grignon; nine valves and carapaces from the Lutetian of Damery; two carapaces from the type Sables d'Auvers; eleven valves and carapaces from the Sables de Beauchamp of Moiselles. Io 3828, 9 .

Type locality and horizon : Montmirail; Lutetian.
Stratigraphical range and distribution: Lutetian, Sables d'Auvers of the type locality, Sables de Beauchamp of Moiselles in the Paris Basin; Sables de Lède of Belgium.

Discussion: Ridge no. 4 is strong and runs from the anterior to the posterior; beneath it are two short, but conspicuous ridges. In the specimens from Grignon and Damery (Lutetian) these two ridges do not quite join, the anterior one finishing just above the anterior end of the posterior ridge; in the specimens from Moiselles, however, they actually join. The reticulation between the ridges tends to be slightly stronger in the Moiselles specimens than in the Lutetian ones.

## Cytheretta decipiens Keij

> (Pl. 6, figs 8-Io)

1955 Cytheretta concinna (non. Triebel) Apostolescu: 261, pl. 4, figs 72-74.
1957 Cytheretta decipiens Keij: 133, pl. 6, fig. 8, pl. 10, figs 15-16.
Material: One carapace from the type Sables d'Auvers, five valves and carapaces from the Sables de Beauchamp of Moiselles. Io 3830-32.

Type locality and horizon: Forest (Belgium), Cuisian.
Stratigraphical range and distribution: Cuisian, Lutetian and Ledian of Belgium; Lutetian, Sables d'Auvers, and Sables de Beauchamp of the Paris Basin.

Discussion: It has been decided to retain this in the genus Cytheretta rather than Flexus because of the presence of several minor longitudinal ridges, apart from the three main ones. The ridge pattern is, in fact, very similar to that of $C$. crassivenia and also to C. haimeana, C. scrobiculoplicata and C. bambruggensis. If Keij's supposition is correct, i.e. C. decipiens was the ancestor of Flexus concinnus (Triebel), at least some part of the genus Flexus has clearly been derived from Middle Eocene Cytheretta. The transition can be closely placed to the Bartonian.

## Cytheretta aff. decipiens Keij

(Pl. 6, fig. 3)

Material: One carapace from the Marnes à $P$. ludensis at Chavençon. Io 3833 .
Dimensions: L, o.66; H, 0.34; L/H, I.94.
Discussion: This is clearly related to C. decipiens, but has lost most of the minor longitudinal ridges; there are still several ventral ridges however. This is probably the form called $C$. concinnus by Keij, but it differs from the latter in several respects. However, it could be placed in an evolutionary sequence, which, starting with $C$. decipiens, eventually gave rise to $F$. concinnus. As only one specimen was available for study, this question has been left open.

## Cytheretta haimeana (Bosquet)

$$
\text { (Pl. 6, figs } x, 6)
$$

1852 Cythere haimeana Bosquet: 6r, pl. 2, fig. I4.
1852 Cythere costellata (non. Roemer) Bosquet (pars) : 58.
1955 Cytheretta haimeana (Bosquet) ; Apostolescu: 262, pl. 5, figs 84-85.
1957 Cytheretta haimeana (Bosquet); Keij: 136, pl. 6, fig. 7, pl. 10, figs 7, 8.
Material: One valve from the Lutetian of Damery; ten valves and carapaces from the type Upper Bracklesham Beds; five valves and carapaces from the type Sables d'Auvers; eight valves and carapaces from the Sables de Beauchamp of Moiselles. Io 3834-5.
Type locality and horizon: Grignon; Lutetian IV.
Stratigraphical range and distribution: Cuisian and Lutetian of the Paris Basin (numerous localities) and the type Sables d'Auvers and Sables de Beauchamp of Moiselles; Upper Bracklesham Beds of England.

Discussion: The specimens from Moiselles and Auvers are larger than those from Damery. The longitudinal ridges are more prominent because the cross ridges are not so strongly developed as in the Lutetian forms.

Cytheretta ruelensis sp. nov.
(Pl. 6, figs 4, 7; Pl. 5, figs 4-7)
Derivation of name: From the hamlet of Le Ruel.
Diagnosis: A species of Cytheretta with I2 longitudinal ridges, of which no. 4 and 5 are prominent, and with coarse puncta between the ridges.

Holotype: Io 3837, a female left valve.
Paratype: Io 3838 .
Material: Four carapaces and one left valve.
Type locality and horizon: Le Ruel; Sables de Cresnes.
Stratigraphical range and distribution: So far only known from the type locality.

Description: Sexual dimorphism is very distinct, the males being more elongate. The left valve has an almost straight dorsal margin with a prominent posterior hinge ear. The anterior margin is obliquely rounded; the ventral margin is almost straight; the posterior margin is obliquely rounded. The right valve has a convex dorsal margin and a concave ventral margin. The carapace is narrowly ovate in dorsal view.

The ornamentation consists of I 2 longitudinal ridges with coarse puncta between them. Ridge no. I forms most of the dorsal margin, leaving it towards the anterior where it swings downwards to join a narrow anterior area of reticulation. Ridges 2 and 3 are not strong; towards the posterior no. 2 bifurcates and no. 3 joins the lower and stronger part. No. 4 and 5 are very strong running almost the whole length
of the carapace; a prominent gap is developed between them to the posterior of the sub-central plexus. The sub-central plexus is not very well developed and lies between ridges 4 and 5. There are four rows of coarse puncta between ridges 4 and 5 forming two double rows; there are four more closely packed rows between 3 and 4 ; two between 2 and 3 , and 5 and 6 ; and one between the remaining ridges.

The internal features could not be clearly seen.
Dimensions (Carapace):

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.75 | 0.43 | I.74 | 0.35 |
| Male | 0.85 | 0.44 | I .93 | 0.37 |

Discussion: C. ruelensis shows a similarity to the C. haimeana group, but the ornamentation is quite distinct and unlike any of these in detail. The puncta between the ridges are unlike any other inter-costal ornamentation developed in this group.

One specimen of a related form has been found in a sample from Moiselles (Pl. 7, fig. II). The ridges form the same pattern as in C. ruelensis but they are all of about equal prominence. This is Cytheretta sp.A.

## Cytheretta eocaenica Keij

(Pl. I, fig. 2; Pl. 7, figs I-Io)

1852 Cythere jurinei (non. von Munster); Bosquet: 56 (pars), pl. 2, fig. 9.
1955 Cytheretta jurinei (non. von Munster); Apostolescu: 263, pl. 5, figs 86-89; pl. 6, figs 90-9r.
1957 Cytheretta eocaenica Keij: 134, pl. 6, fig. 6; pl. 10, figs 2-4.
Diagnosis: (After Keij, 1957) : 'A species of the genus Cytheretta with the following characteristics; anterior margin obliquely rounded, obtusely angular ventrally; with horizontal rows of rounded depressions posteriorly; inner margin with three inward protrustions in the ventral half of the valve.'

Material: rog valves and carapaces from the Sables de Lède of Bambrugge were available for study, donated by Dom. R. Rome, together with nine valves and carapaces from the Lutetian IV of Damery. Io 3839-44.
Type locality and horizon: Grignon; Lutetian IV.
Stratigraphical range and distribution: Cuisian and Lutetian of the Paris Basin; Lutetian and Ledian of Belgium; Upper Bracklesham Beds of England.

Discussion: Keij describes the ornamentation as consisting of 3-5 horizontal rows of rounded depressions in the postero-ventral part of the valve with additional widely scattered depressions in the female. The specimens from Bambrugge have some nine rows of pits in the postero-ventral region and some five in the antero-ventral region. There is a smooth area near the centre of the valve representing the subcentral plexus from which run two prominent rows of pits towards the direction of the anteroventral angle. The Damery specimens fit Keij's description with five postero-ventral rows of pits; the more ventrally placed pits, as developed at Bam-
brugge, are absent. However, the two prominent anterior rows can also be distinguished.

Another feature of the Bambrugge sample is the presence of a few very large individuals, about I in 8 . These are similar in shape and ornamentation to the smaller specimens. The smaller individuals are definitely adults: the hinge, sexual dimorphism, thick shell and inner margin are all well developed. This is probably an example of post-maturation moulting.

Dimensions:

|  | L | H | W | L/H |
| :--- | :---: | :---: | :---: | :---: |
| Female (normal) | 0.78 | 0.47 | 0.40 | I .66 |
| Female (Iarge) | 0.93 | 0.59 | 0.49 | I .58 |

Sex ratio: I : 3 .

## Cytheretta oligocaenica sp. nov.

(Pl. 8, figs $\mathrm{I}-\mathrm{I} 3$ )
Derivation of name: From Oligocene; refers to the strata in which it is found.
Diagnosis: A species of Cytheretta with an obliquely rounded anterior margin and slightly convex ventral margin in the left valve; ornamentation consists of up to 8 rows of pits in the postero-ventral region; there is often an ill-defined sulcus in the postero-lateral position.

Holotype: Io 3845 , a female left valve.
Paratypes: Io 3846-9.
Material: Couches du Phare (Biarritz), 55 valves and carapaces; Couches de l'Atalaye (Biarritz), II valves and carapaces; St. Geours de Maremne, 9 valves and carapaces; Blaignan, 5 carapaces.

Type locality and horizon: Biarritz; Couches du Phare (RO 27I); Stampian.
Stratigraphical range and distribution: Couches de l'Atalaye and Couches du Phare, Biarritz; Faluns Bleues of St. Geours de Maremne; Argile à algues, Blaignan.

Description : Sexual dimorphism is distinct. Sex ratio, r:3. The left valve has a prominent posterior hinge-ear and a convex dorsal margin; the anterior margin is obliquely rounded; the ventral margin is slightly convex; the posterior margin is obliquely rounded. The greatest height is just to the anterior of centre. The right valve has its greatest height about one quarter of the way from the posterior margin and this results in a slight triangular shape as the almost straight dorsal margin slopes towards the anterior margin; the ventral margin is concave.

The ornamentation consists of up to 8 rows of pits in the postero-ventral region. An ill-defined sulcus is often present in the postero-lateral position.

The antero-dorsal lobe of the hinge of the left valve is swollen; the antero-ventral lobe is large and prominent; the antero-median tooth is large; the postero-median
swelling is prominent. The anterior tooth of the right valve is crescentic-shaped in lateral view; in dorsal view both teeth of the right valve are large and squat (Plate 8, Fig. 8-I3).

The inner margin has a narrow anterior indentation and small ventral and posterior indentations; the anterior segment is semi-circular; the median segment is long with a gentle upward slope; the posterior segment is short and semi-circular. There are some 35 anterior and 17 ventral radial pore canals. The posterior radial pore canals are very closely packed and there are about 80 of them; they are not divisible into two groups. The selvage is very close to the anterior margin; there is a small posterior flange groove and a larger ventral one; a weak list is present.

As with C. cocaenica, there are a few very large individuals, about $10 \%$.
Dimensions:

|  | L | H | W | L/H |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.85 | 0.53 | 0.5 I | I .60 |
| Male | 0.86 | 0.49 | 0.4 I | I .7 I |
| Large form, male | 0.98 | 0.58 | - | I .70 |

Discussion: This is very similar to C. eocaenica Keij. It differs in shape; the antero-ventral angle is rounded and not angular as in C. eocaenica, the ventral margin is slightly convex, not straight, and the greatest height is just to the anterior of centre, whereas it is about one third of the way from the anterior in C. eocaenica. The right valve is much higher in the posterior in C. oligocaenica. There are more anterior radial pore canals in the latter, 35 compared with 27-30. The inner margin is similar in both species, and in this respect they differ from C. jurinei (von Munster), which has a very large and circular posterior indentation.

See also C. geoursensis sp. nov.

## Cytheretta geoursensis sp. nov.

(Pl. Io, figs $I, 3,5$ )
Derivation of name: From St. Geours de Maremne.
Diagnosis: A large species of Cytheretta with a prominent posterior hinge ear, convex ventral margin of left valve, and a finely punctate outer surface.

Holotype: Io 3850 , a female left valve.
Paratypes: Io 385I-2.
Material: Eight valves and carapaces.
Type locality and horizon : Marnière d'Escornbéou, near St. Geours de Maremne (Aquitaine Basin); Faluns bleues, Oligocene(?) (Chattian?).
Stratigraphical range and distribution: So far only known from the type locality.

Description: Sexual dimorphism is distinct; sex ratio, I:3. The left valve has a very prominent posterior hinge ear; the dorsal margin is strongly convex; the anterior margin is obliquely rounded; the ventral margin is strongly convex, par-
ticularly towards the posterior; the posterior margin is obliquely rounded. The right valve has a slightly convex dorsal margin and a slightly concave ventral margin.

The whole outer surface of the carapace is covered with a very superficial appearing punctation. Two or three rows of pits in the postero-lateral position can be seen on some specimens, and one right valve has these quite prominently developed.

The hinge, inner margin, selvage and list are as for C. oligocaenica. There are 27 anterior radial pore canals, but the exact number of posterior radial pore canals could not be determined.

Drmensions:

|  | L | H | W | L/H |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.98 | 0.58 | 0.60 | I .69 |
| Male | I .07 | 0.58 | 0.50 | I .84 |

Discussion: This could perhaps be regarded as a post-maturation moult stage of C. oligocaenica sp. nov. similar to those already described. However, unlike these, this is not merely a larger version of the small forms. It differs from C. oligocaenica in shape, particularly the strongly convex ventral margin of the left valve; in ornamentation; and in the number of anterior radial pore canals ( 27 compared with 35 ).

## Cytheretta carita sp. nov.

## (Pl. 9, figs 5, 8, 9-II ; Pl. 10, fig. 7. Text-fig. 14)

Derivation of name: Latin-carita, to be without or to be deprived; refers to the lack of ornamentation.

Diagnosis: A smooth species of Cytheretta with an obliquely rounded anterior margin and two 'dimples' in the posterior.

Holotype: Io 3853 , a female left valve.
Paratypes: Io 3854-8.
Material: 39 valves and carapaces from the type Auversian; 57 from Moiselles; 5 from Le Ruel, Sables de Cresnes; I from the Marnes à $P$. ludensis at Verzy.

Type locality and horizon : Carriere de Moiselles; Sables de Beauchamp.
Stratigraphical range and distribution: 'Bartonian' of the Paris Basin.
Description: Sexual dimorphism distinct; sex ratio, I : 2.5. The dorsal margin of the left valve has a prominent posterior hinge ear, is straight until about the midpoint when it slopes down to the anterior margin, which is very obliquely rounded. The ventral margin is slightly convex and curves into the posterior margin, which is rounded. The dorsal margin of the right valve is more irregular; a slight hinge ear is present at the posterior and the anterior tooth projects beyond the margin. There is a marked concavity between the hinge ear and the posterior margin. The ventral margin is slightly concave. In dorsal view it is ovate.

The valve is smooth. At the posterior are two dimples, one in the postero-ventral angle and the other higher along the posterior margin.

In the hinge of the left valve, the antero-ventral lobe is weakly developed, leaving the anterior socket almost open ventrally; the antero-dorsal lobe is flat to lobate and small; the antero-median tooth is large; the postero-median swelling small. In the right valve the anterior tooth is large and the posterior tooth is slightly reniform.

The anterior indentation of the inner margin is narrow; the ventral deep and prominent; and the posterior broad, but deep. The median segment is almost flat; the posterior segment is steeper, but not very pronounced. The muscle scars are normal, the two ventral scars being close together. They are situated in a slight pit.

The selvage runs along the anterior margin of both valves, so there is no anterior flange groove. A ventral flange groove is well developed, as well as a small posterior one. A very weak list is present along the ventral and posterior duplicature.


Fig. 14. Cytheretta carita sp. nov.; female right valve; $\times 75$.
Dimensions:

|  | L | H | W | L/H |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.87 | 0.55 | 0.43 | I.58 |
| Male | 0.93 | 0.53 | 0.4 I | I .75 |

Discussion: This differs from other smooth Cytheretta species such as C. rhenana Triebel by its shape and the presence of the posterior dimples. It shows a very close relationship to C. eocaenica, but lacks the longitudinal rows of pits of the latter.

## Cytheretta cellulosa sp. nov.

(Pl. 9, figs I-4, 6, 7)
Derivation of name: Latin-cellulosus, full of little cells, referring to the ornamentation.

Diagnosis: A species of Cytheretta with I3 rows of pits which converge at the posterior; dorsal area is smooth.

Holotype: Io 3859, a female left valve.
Paratypes: Io 3860-63.
Material: Eight valves and carapaces from the type Auversian; fourteen valves and carapaces from Moiselles.

Type locality and horizon: Auvers-sur-Oise; Sables d'Auvers.
Stratigraphical range and distribution: Auversian of the Paris Basin.
Description: Sexual dimorphism is pronounced; sex ratio, $\mathrm{I}: 3$. The dorsal margin of the left valve has a prominent posterior hinge ear and is convex. The anterior margin is slightly obliquely rounded; the ventral margin is straight in the central portion; the posterior margin is very obliquely rounded. In the male, the ventral margin has a very straight appearance. The right valve has a concave ventral margin. Carapace is ovate in dorsal view.
The ornamentation of the left valve consists of 13 rows of small pits. In the posterior region these rows converge and merge into one another; the pitting is very fine. In the central region the rows are distinct and consist of a single line of pits larger in the centro-dorsal region. The central rows converge upon an ill-defined sub-central plexus, which is almost smooth. To the anterior of this the rows consist of double rows of puncta; there are five of these, together with three ventral rows of single puncta which are continuous along the ventral region. The dorsal area is smooth. The right valve is similar except that there are single rows of pits in the anterior region.

The hinge of the left valve has a swollen antero-dorsal lobe; a small antero-ventral lobe so that the anterior socket is virtually open ventrally, as is the posterior socket; a large antero-median tooth; and a small inconspicuous postero-median swelling. The anterior tooth of the right valve is large, and the posterior tooth is prominent.
The inner margin could not be clearly seen. There are some 20 anterior radial pore canals. The central muscle scars are in a slight pit, and the two ventral ones are close together. One very prominent dorsal muscle scar can be seen above the fulcral point. The selvage runs close to the anterior margin; there is a ventral flange groove and a small posterior one. A weak list is present along the anterior, ventral and posterior parts of the duplicature.
Dimensions:

|  | L | H | W | L/H |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.80 | 0.49 | 0.38 | I.65 |
| Male | 0.93 | 0.5 I | 0.43 | I.82 |

Discussion: C. cellulosa bears a ressemblance to C. tenuipunctata (Bosquet), but the pattern of pits is different and the outline of the valve is completely different. C. eocaenica Keij from the Ledian of Bambrugge often develops pits over a large area, although never to the same extent as here. The shape, however, is similar, and it is thought likely that $C$. eocaenica is the ancestor of $C$. cellulos $a$, with such forms as those from Bambrugge as intermediates.

## Cytheretta aff. cellulosa

1968 Cytheretta minor (non Lienenklaus) Haskins: 167, pl. 1, figs 30-35.
Discussion: Haskins records this from the Barton Beds in Alum Bay. In many respects it appears to be intermediary between C. cellulosa and C. minor.

## Superspecies Cytheretta laticosta (Reuss)

Diagnosis: A group of species of the genus Cytheretta characterized by three longitudinal ridges. The dorsal ridge is convolute; the median ridge contains four depressions along its ventral side; the ventral ridge is the most prominent of a group of ridges developed in the ventral part of the valve.

Description : The carapace generally has a massive appearance with a thick shell; it is strongly inequivalve, and sexual dimorphism is pronounced. In the left valve there is a prominent posterior hinge ear. In the right valve the anterior tooth projects beyond the margin and che ventral margin is concave. In dorsal view the carapace is swollen posteriorly in both males and females, but this is more pronounced in the latter.

The ornamentation consists predominantly of three thick longitudinal ridges. The dorsal ridge runs along the margin, but does not reach the anterior margin; the median ridge swells in the central region and contains four depressions on its ventral side, each of which has a normal pore canal opening into it. This runs from the anterior margin to the posterior, where it curves upwards to form a margin to the hinge ear. The ventral ridge also contains four depressions with normal pore canals, much better seen in the right valve. In the left valve this ridge is really the most pronounced of a series of ventral ridges, of which there are seven in all. In the right valve the lower ventral ridges are indistinct or absent, and this gives the whole valve a strongly tri-costate appearance. A prominent marginal rim runs around the anterior margin and the anterior portion of the ventral margin. In the right valve there is a posterior marginal rim. There are some eight marginal antero-ventral denticles, each of which bears a radial pore canal, and three posterior ones. The latter are larger in the right valve. The whole surface is finely punctate, although this can only be seen on well preserved specimens.

The hinge of the left valve has a swollen, knob-like, antero-dorsal lobe; the anteroventral lobe is small; the antero-median tooth is prominent; postero-median swelling is small. In the right valve the anterior tooth is large and the posterior tooth circular in plan.

The selvage is prominent, particularly in the right valve; there is a well developed flange groove in the anterior, ventral, and posterior; and a list is present in the postero-ventral region. There are some 32 anterior radial pore canals, 20 ventral, and 18 posterior; and 29 normal pore canals which are arranged in sympathy with the ornamentation (Text Fig. 15). The central and dorsal muscle scars are as for the genus.

## Cytheretta laticosta (Reuss)

(Pl. I, fig. 3; Pl. Io, figs $2,4,6,8,9$; Pl. I2, figs I-2 5; Text-fig. I5).
1850 Cypridina laticosta Reuss: 87, pl. 11, fig. 13.
1857 Cythere plicata var. laticosta (Reuss); Jones: 32, pl. 5, fig. 8 (pars).
1889 Cytheve plicta var. laticosta (Reuss); Jones and Sherborn: 29 (pars).
1957 Cytheretta laticosta (Reuss); Keij: 137, pl. 18, figs 15-18; pl. 21, fig. 16.
1968 Cytheretta laticosta (Reuss); Haskins: 166 (pars), pl. 2, figs 23, 27, 28.

Diagnosis: A member of the superspecies C. laticosta with an evenly rounded anterior margin, convolute dorsal ridge and small areas of coarse puncta around the median and ventral ridges.

Material: Three carapaces from the Lower Barton Beds of Alum Bay; numerous specimens from the Middle and Upper Barton Beds of Barton, and Alum Bay; fifteen valves and carapaces from the Marnes à P. ludensis of Verzy, and five from Chavençon. Io 3864-70.

Type locality and horizon: Barton Clay of Barton (see discussion).
Stratigraphical Range and distribution: Barton Clay of Barton, Alum Bay and Whitecliff Bay; Marnes à P. ludensis of Verzy and Chavençon; Argile d'Asche of Oedelem (Belgium).

Description: Sex ratio, i : i•6. The carapace is massive, the shell is thick. The dorsal ridge is thick with convolutions forming some six depressions, which bear normal pore canals. The median ridge has a prominent swelling in the central part and has an area of coarse puncta around the four depressions. The ventral ridge likewise has an area of coarse puncta.

The inner margin has a narrow and deep anterior indentation, particularly in the right valve, and a prominent ventral one. The anterior segment is sharply rounded. The median and posterior segments are inseparable; they slope up to the posterior indentation, which is quite close to the ventral margin.

Dimensions:
Left valve Right valve

|  | L | H | L/H | W | L | H | L/H |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Female | $0.80 \pm 0.02$ | $0.50 \pm 0.01$ | $\mathrm{I} .60 \pm 0.04$ | 0.46 | 0.79 | 0.42 | I .88 |
| Male | $0.86 \pm 0.02$ | $0.49 \pm 0.0 \mathrm{I}$ | $\mathrm{I} .76 \pm 0.04$ | 0.45 | 0.89 | 0.46 | I .94 |

Discussion: Reuss described this as coming from the London Clay of Barton, Hampshire. This relates to the idea prevalent in the early Igth century that the clay at Barton was of the same age as that at London; in fact, the London Clay is Lower Eocene, while the Barton Clay is Upper Eocene.


Fig. 15. Cytheretta laticosta (Reuss) showing distribution of normal pore canals in relationship to ornamentation; $\times 75$.

## Cytheretta forticosta sp. nov.

(Pl. II, figs $I-4,8,9$; Pl. 12, figs 6-I2)
1857 Cythere plicata (non. von Munster); Jones: 32 (pars).
1968 Cytheretta laticosta (Reuss); Haskins: 166 (pars), pl. 2, figs 19-22, 24-26, 29.
Derivation of name: Latin-fortis, strong; costa, ridge. Refers to the three strong longitudinal ridges.

Diagnosis: A member of the superspecies C. laticosta with an obliquely rounded anterior margin and simple median ridge.

Holotype: Io 387 I , a female left valve.
Paratypes: Io 3872-8.
Material: Numerous specimens from the localities mentioned below.
Type locality and horizon: Fisher Beds r7-18, Upper Bracklesham Beds, Whitecliff Bay.

Stratigraphical range and distribution: Upper Bracklesham Beds of Whitecliff Bay, Selsey Bill, and Bramshaw (New Forest); Sables de Cresnes, Le Ruel.

Description: Sex ratio, I :2.5. The carapace is massive. The left valve of the female has a circular outline; the dorsal margin is strongly convex; the anterior margin is obliquely rounded; the ventral margin is short and straight; the posterior margin is very obliquely rounded. In the right valve the dorsal outline is irregular, and the ventral margin is concave.

The dorsal ridge has five depressions, each of which bears a normal pore canal. The four pits on the median ridge are simple; those on the ventral ridge are prominent in both valves. The surface of the valve is punctate. In the right valve the ventral group of ridges are distinct in the anterior and posterior regions.

The inner margin is similar to that of $C$. laticosta except that the joint median and posterior segments have two undulations.

Dimensions:

|  | Left valve |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | W | L | $H$ | L/H |
| Female | $0.77 \pm 0.03$ | $0.52 \pm 0.02$ | $\mathrm{I} .46 \pm 0.04$ | 0.52 | 0.83 | 0.45 | I .84 |
| Male | $0.87 \pm 0.03$ | $0.54 \pm 0.02$ | $\mathrm{I} .62 \pm 0.05$ | 0.52 | 0.90 | 0.48 | I .88 |

Cytheretta porosacosta sp. nov.
(Pl. II, figs $5-7$; Pl. I2, figs 3,4 )
1857 Cythere plicata (non. von. Munster); Jones: 32 (pars), pl. 4, fig. 16; pl. 5, fig. 8. 1889 Cythere plicata (non. von Munster); Jones and Sherborn: 29 (pars), pl. I, fig. 18. 1968 Cytheretta laticosta (Reuss); Haskins: p. 166 (pars).

Derivation of name: Latin-porosus, full of holes; costa, ridge. Refers to the heavily punctate ornamentation.

Diagnosis: A member of the superspecies $C$. laticosta with an evenly rounded anterior margin, simple ridge, and wide areas of large puncta.

Holotype: Io 3879 , a female left valve.
Paratypes: Io 3880-83.
Material: Numerous valves from the localities mentioned below.
Type locality and horizon: Colwell Bay, Isle of Wight; Middle Headon Venus Bed.
Stratigraphical range and distribution: Brockenhurst Beds of Brockenhurst and Whitecliff Bay; Middle Headon Beds of Colwell Bay, Headon Hill, Whitecliff Bay, Milford, and Brockenhurst.
Description: The dorsal margin of the left valve is slightly irregular due to the over-reach of the dorsal ridge; otherwise it is straight to slightly convex. The anterior margin is evenly rounded; the ventral margin is slightly concave; and the posterior margin obliquely rounded.

In the left valve the dorsal ridge has several faint depressions, but is fairly simple. The median ridge is narrow, with four very faint depressions on the ventral side. There is no strong ventral ridge. In the right valve however, the ventral ridge is distinct due to the absence of the lower ventral ridges. Large areas of coarse puncta are developed amongst the ventral group of ridges and around the median ridge.

Dimensions:

|  | Left valve |  |  |  | Right valve |  |
| :--- | :---: | :---: | :--- | :---: | :---: | :---: |
|  | L | H | H | L | H | $\mathrm{L} / \mathrm{H}$ |
| Female | $0.74 \pm 0.02$ | $0.44 \pm 0.01$ | $\mathrm{I} .68 \pm 0.025$ | 0.74 | 0.38 | 1.92 |
| Male | $0.78 \pm 0.02$ | $0.42 \pm 0.01$ | $\mathrm{I} .84 \pm 0.04$ | 0.82 | 0.40 | 2.05 |

Discussion: The three species described are only part of the superspecies C. laticosta. Other forms not studied are found in the London Clay of the London and Hampshire basins and the Lower and Middle Bracklesham Beds.

The most noticeable difference between these species is the shape of the carapace. This is most marked in the female dimorph. The species represent three quite distinct groups (Text-fig. 16). The $\mathrm{L} / \mathrm{H}$ ratio is:

|  | Female | Male |
| :--- | :---: | :---: |
| C. forticosta | $\mathrm{I} \cdot 46 \pm 0.04$ | $\mathrm{I} .62 \pm 0.05$ |
| C. laticosta | $\mathrm{I} .60 \pm 0.03$ | $\mathrm{I} .76 \pm 0.04$ |
| C. porosacosta | $\mathrm{I} .68 \pm 0.025$ | $\mathrm{I} .84 \pm 0.04$ |

The anterior margin changes from obliquely rounded in C. forticosta to evenly rounded in C. laticosta and C. porosacosta.

The three longitudinal ridges are more complex in C. laticosta. The dorsal ridge is convolute and complicated. The four depressions in the median ridge are prominent and punctate; in C. forticosta there are only four large puncta and no depressions; in C. porosacosta the depressions are almost absent. The ventral ridge has a prominent central area with coarse puncta; these are not present in C. forticosta, while in C. porosacosta the puncta cover a large area of the valve. In the right valve of C. forticosta the ventral group of ridges are stronger than in C. laticosta and C. porosacosta.

The trends seen in these three species are, therefore:
(i) Change from a rounded to a more elongate shape.
(ii) Anterior margin from obliquely rounded to evenly rounded.
(iii) Development of coarse puncta, especially around the median and ventral ridges.

The group of specimens from Le Ruel have a mean $\mathrm{L} / \mathrm{H}$ ratio of $\mathrm{I} \cdot 43$ and have a more rounded appearance than the English C. forticosta. The specimens from Selsey Bill and Bramshaw are more elongate, with a mean ratio of $\mathrm{I} \cdot 50$. The Whitecliff


Fig. i6. Size distribution of species of the superspecies C. laticosta (Ruess).

Bay specimens have a mean of $1 \cdot 46$ and have an even distribution. There is considerable overlap between these specimens, however, which does not occur between these specimens of $C$. laticosta and C. porosacosta.

The variation in size is most noticeable between C. porosacosta on the one hand and C. laticosta and C. forticosta on the other. This is thought to be environmental because $C$. porosacosta is found in beds with a mixed marine and brackish water fauna. The thinner shell of C. porosacosta and the general weakness of the three ridges is probably also connected with this. The specimens of $C$. forticosta from Bramshaw and Selsey are seen to be smaller than those from Whitecliff Bay; and C. laticosta from the Ludian of the Paris Basin are smaller than those from the Barton Clay. This may be environmental. The specimens from Le Ruel show a large range in size, due perhaps to the nature of the Sables de Cresnes, which are coarse-grained current-bedded sands, often with rolled macro-fossils.

Eventually, specimens of an intermediate nature may be found between these three species, in which case they will become subspecies. It is thought highly likely that such intermediates exist, but at the moment there are present three distinct groups with no overlap.

## Superspecies Cytheretta tenuipunctata (Bosquet)

The superspecies $C$. tenuipunctata comprises a group of ostracods with similarities in shape of lateral view, ornamentation, and internal structures. The following species and subspecies are included:
C. tenuipunctata tenuipunctata (Bosquet)
C. tenuipunctata absoluta subsp. nov.
C. tenuipunctata lirata subsp. nov.
C. tenuistriata tenuistriata (Reuss)
C. tenuistriata ornata subsp. nov.
C. bernensis Oertli
C. buttensis sp. nov. buttensis subsp. nov.
C. buttensis reticulata subsp. nov.
C. minipunctata sp. nov.

The following are tentatively included:
C. triebeli Oertli
C. variabilis Oertli
C. ramosa ramosa (Lienenklaus)
C. ramosa sublaevis Triebel

There are further groups of ostracods from the Oligocene of western Europe which are also closely related to the superspecies. These are discussed below.

Diagnosis: A superspecies of the genus Cytheretta with up to I3 longitudinal ridges, often stronger in the ventral half of the valve, which form a regular pattern, although differing slightly in detail between species. There are three ridges in the anterior part which run from the region of the sub-central plexus towards the antero-ventral angle. In lateral view the carapace is elongate with pronounced sexual dimorphism;
in dorsal view it is ovate or tapered towards the anterior. The valves are not strongly inequivalve.

Description: The shape varies, but in general it is elongate in lateral view. In dorsal view it is usually ovate, or slightly triangular with its apex at the anterior. Sexual dimorphism is pronounced; sex ratio, I:2. The valves are inequivalve, but not strongly so.

Up to I3 longitudinal ridges are developed, which may be strong or weak. In some species no ridges are present in the dorsal half of the valve. The ornamentation between the ridges varies from species to species. A complete development is seen in Text-fig. 17.

Ridge no. r runs from near the posterior hinge ear, disappearing to the anterior of the sub-central plexus. No. 2 is often formed of a series of short curved ridges, usually broken and bifurcating. No. 3 joins no. 2 in the posterior, runs above the sub-central plexus, and just to the anterior of it joins no. a. In some species, and particularly in the right valve, ridge a is very prominent, sloping sharply towards the antero-ventral angle. The sub-central plexus is an irregular, smooth area, varying from species to species, but usually prominent. Three parallel ridges, $a, b$, and $c$, run from the sub-central plexus towards the antero-ventral angle; these are diagnostic of the superspecies. There are another three parallel ridges, 4,5 , and 6 to the posterior of the sub-central plexus. Ridge no. 7 joins no. 4 at the posterior and no. 8 at the anterior. Ridges $8-13$ are approximately parallel to the ventral margin. The ridges form a complicated pattern at the posterior, seen in Text-fig. 17. Ridges 9-I3 disappear amongst fine puncta at the posterior.

The antero-dorsal lobe of the hinge of the left valve is prominent and slightly swollen; the antero-ventral lobe is prominent; the antero-median tooth is well developed, but the postero-median swelling is virtually absent. In the right valve the anterior tooth is slightly reniform in shape; in dorsal view the two teeth appear to be almost equal in size.

The selvage is prominent along the ventral and posterior margins. A wide flange groove with a well marked flange is present in the ventral region; in the posterior the flange groove is narrow and a small fringe is developed. Along the anterior


Fig. 17. Ridges of the superspecies Cytheretta tenuipunctata (Bosquet). The specimen is C. tenuistriata ornata subsp. nov; $\times 75$.
margin a few very small denticles are present; a radial pore canal opens from each of them. There are some 35 anterior radial pore canals and some 40 closely spaced posterior pore canals. The inner margin varies slightly from species to species.

## Cytheretta tenuipunctata (Bosquet)

Diagnosis: A species of the superspecies $C$. tenuipunctata with a prominent subcentral plexus and a medium to coarse pitting between the ridges, the pits often being in double rows in the median part of the valve. The ridges are strongly developed.

Discussion: This was described by Bosquet from the Argile à N. comta of Belgium. It is very similar to C. tenuistriata (Reuss), and Keij (I957) believed that the two were synonymous. This was because of the similarities in ornamentation. The two species are here regarded as distinct, but are placed within the same superspecies. C. tenuistriata is a much larger ostracod than C. tenuipunctata, but in itself this need not be important. In the Paris Basin however, the two co-exist without intermediaries, so that the difference in size is very obvious; thus they formed two separate populations which must be assumed to be specifically distinct. The ornamentation between the ridges consists of a coarser pitting in C. tenuipunctata than in $C$. tenuistriata.

## Cytheretta tenuipunctata tenuipunctata (Bosquet)

1852 Cythere jurinei (non. von Munster); Bosquet: 56 (pars).
1852 Cythere jurinei var. tenuipunctata Bosquet: 56, pl. 2, fig. ıo.
1957 Cytheretta tenuipunctata (Bosquet) ; Keij: 138, pl. 5, fig. 21 ; pl. 6, fig. 5.
Type locality and horizon: Berg, near-Kleine Spouwen, Belgium; Argile à N. comta (Rupelian).

Stratigraphical range and distribution: Upper Tongrian (?) and Lower Rupelian of Belgium.

Dimensions: (After Keij):

$$
\begin{array}{ll}
\text { Lectotype (Male R) } & 0.96 \times 0.47 \\
\text { Female L } & 0.88 \times 0.5 \mathrm{I}
\end{array}
$$

Discussion: Keij (1957) has selected a lectotype and redescribed species as having $6-8$ ridges which gradually vanish towards the anterior and posterior margins; between the ridges are fine pits, mostly in two rows; towards the dorsal margin the surface is pitted, but without ridges; the areas along the anterior, posterior, and dorsal margins are smooth; and a sub-central plexus is well developed.
C. tenuipunctata tenuipunctata differs from the two subspecies described below by the absence of the dorsal ridges.

Cytheretta tenuipunctata absoluta subsp. nov.

$$
\text { Pl. I4, figs I-4, 6, } 7 \text {; Text-fig. I8) }
$$

Derivation of name: Latin-absolutus, complete; refers to the ornamentation which completely covers the valve, unlike C. tenuipunctata tenuipunctata.

Diagnosis: A subspecies of C. tenuipunctata in which the full I3 ridges of the superspecies $C$. tenuipunctata are developed; the ornamentation between the ridges consists of a fine pitting, in double rows in the median and dorsal parts of the valve, and single rows between the ventral ridges.

Holotype: Io 3884, a female left valve.
Paratypes: Io 3885-9.
Material: 55 adult valves and carapaces and 68 larval stages from Cormeilles.
Type locality and horizon : Cormeilles-en-Parisis; Marnes à Huîtres.
Stratigraphical range and distribution : Marnes à Huîtres of the Paris Basin.
Description: The dorsal and ventral margins of the valves are sub-parallel, particularly in the left valve. In the latter there is a prominent posterior hinge ear; the dorsal margin is slightly convex; the anterior margin is evenly rounded; the ventral margin is straight or slightly concave; the posterior margin obliquely rounded In the right valve the ventral margin is concave and there is a concavity in the postero-dorsal position. In dorsal view the carapace is ovate.

The ridges are well defined, particularly in the right valve. The ornamentation between the ridges consists of a fine pitting. Between ridges $1,2,3$ and 4,6 and 7 , $\mathrm{a}, \mathrm{b}, \mathrm{c}$, there is a double row of pits; between the ventral ridges there is a single row. The anterior region is reticulate.
The inner margin (Text-fig. 18) has a broad anterior and posterior indentation and a well marked ventral indentation. The anterior segment is rounded, and the joint median and posterior segments are undulating.

Two larval stages have been recognised (Text-fig. 19). In these the complete ridge pattern of the adult is developed with small puncta between them; these are in rows of three between ridges no. 6 and 7 , and in double rows between the others. Ridges 8 and 9 are very strong in the posterior region and in larval stage 7 there is a distinct swelling in this region.

Dimensions:

|  | Left valve |  |  |  | Right valve |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | W | L | $H$ | L/H |
| Female | $0.87 \pm 0.03$ | $0.49 \pm 0.01$ | $I .76 \pm 0.05$ | 0.43 | 0.87 | 0.46 | $I .89$ |
| Male | $I .00 \pm 0.02$ | $0.5 \mathrm{I} \pm 0.01$ | $I .96 \pm 0.02$ | 0.43 | 0.98 | 0.50 | $I .96$ |

Discussion: This subspecies differs from C. tenuipunctata tenuipunctata in the larger number of ridges, caused by their presence in the dorsal regions. It differs from C. tenuipunctata livata subsp. nov. in having a slightly different shaped dorsal margin, the latter having a weak anterior hinge ear in the left valve, and in the ornamentation between the ridges which show a great deal of variation in C. tenuipunctata livata.


Fig. 18. Cytheretta tenuipunctata (Bosquet) absoluta subsp. nov.; female right valve; $\times 75$.


Fig. 19. Size distribution of the adults and larval stages of Cytheretta tenuipunctata (Bosquet) absoluta subsp. nov.

Cytheretta tenuipunctata lirata subsp. nov. (Pl. I4, figs 5, 8-10; Pl. I5, fig. Io; Pl. I6, fig. 4)
1895 Cythere jurinei (non. von Munster); Lienenklaus: 8 (pars).
Derivation of name: Latin-lirata, earth or ridge formed by ploughing; refers to the ornamentation.

Diagnosis: A subspecies of C. tenuipunctata in which the full 13 ridges of the superspecies $C$. tenuipunctata are developed; the ornamentation between the ridges varies from pitting to reticulation; a weak hinge ear is developed in the left valve.

Holotype: Io 3890 , a female left valve.
Paratypes: Io 3891-95.
Material: 37 valves from Auvers-St-George.

Type locality and horizon: Auvers-St-George; Stampian.
Stratigraphical range and distribution: Stampian of the Paris Basin.
Description: The shape of the dorsal margin of the left valve is convex with two slight concavities to the anterior and posterior of the posterior and anterior hinge ears respectively. Otherwise the shape is similar to C. tenuipunctata absoluta. The I3 ridges are developed, although a few specimens show a smooth area in the anterodorsal region, but this is small. Ornamentation between the ridges shows a large amount of variation; pits are usually developed, sometimes in a double row, but more often in a single row; in other specimens a fine reticulation is present, and in others the longitudinal ridges are very strong with a relatively inconspicuous ornamentation between them. The sub-central plexus is well developed. There is an anterior area of reticulation. The inner margin is similar to that of $C$. tenuipunctata absoluta.

Dimensions:

|  | Left valve |  |  |  |  |  |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | $\mathrm{L} / \mathrm{H}$ | $\frac{1}{2} \mathrm{~W}$ | L | H | $\mathrm{L} / \mathrm{H}$ |  |  |  |  |  |
| Female | $0.89 \pm 0.03$ | $0.49 \pm 0.0 \mathrm{I}$ | $\mathrm{I} .82 \pm 0.03$ | 0.29 | 0.90 | 0.45 | 2.00 |  |  |  |  |  |
| Male | 0.96 | 0.49 | I .97 | 0.29 | 0.98 | 0.48 | 2.04 |  |  |  |  |  |

Discussion: See $C$. tenuipunctata absoluta subsp. nov.

## Cytheretta tenuistriata (Reuss)

Diagnosis: A species of the superspecies C. tenuipunctata of large size, with well developed sub-central plexus and distinct ornamentation between the ridges.

## Cytheretta tenuistriata tenuistriata (Reuss)

(Pl. 16, figs 5, 7)
1853 Cytherella tenuistriata Reuss: 676, pl. 9, fig. 1 .
1905 Cythereis jurinei (non. von Munster); Lienenklaus: 3I (pars).
1952 Cytheretta tenuistriata (Reuss); Triebel: 22, pl. 3, fig. 12-15.
1956 Cytheretta tenuistriata (Reuss); Oertli: 6i, pl. 6, fig. 163-165.
Material: Specimens from several localities around Weinheim; Io 3896-7.
Type locality and horizon: Weinheim, Mainz Basin; Unterer Meeressand.
Stratigraphical range and distribution: Unterer Meeressand of the Mainz Basin, Blaue Ton of Switzerland; Rupelian.

Diagnosis and description: The male has an anterior hinge ear in the left valve which, together with the posterior hinge ear, gives the dorsal margin an undulating appearance with two concavities. The anterior hinge ear is not present in the female, so the dorsal margin of the left valve is regular, and the valve has its greatest height close to the anterior end. The ornamentation is not strong; the ridges are weakly defined and in between them are double rows of small pits. The anterior and posterior areas are smooth.

Dimensions (After Triebel):

$$
\begin{array}{ll}
\text { L Female } & \mathrm{I} \cdot 08-\mathrm{I} \cdot \mathrm{I} 3 \mathrm{~mm} \\
\text { Male } & \mathrm{I} \cdot 22-\mathrm{I} \cdot 28 \mathrm{~mm}
\end{array}
$$

Discussion: See C. tenuistriata ornata below.

## Cytheretta tenuistriata ornata subsp. nov.

(Pl. 13, figs I-I2; Text-figs I7, 20)
1852 Cytheve jurinei var. tenuipunctata Bosquet: 56 (pars).
1895 Cythere jurinei (non. von Munster); Lienenklaus: 8 (pars).
Derivation of name: Latin-orno, ornamented; refers to the strong ornamentation.

DIAGNOSIS: A subspecies of $C$. tenuistriata with strong ornamentation.
Holotype: Io 3898 , a female left valve.
Paratypes: Io $4020-7$.
Material: 32 valves from Auvers-St-George, 3 valves from Morigny; Io 3899.
Type locality and horizon: Auvers-St.-George; Stampian.
Stratigraphical Range and distribution: Stampian of Auvers-St.-George, Jeurre, and Morigny in the Paris Basin.

Description: The dorsal margin of the left valve of both the male and the female is almost straight with two slight concavities, one to the anterior of the posterior hinge ear and the other to the posterior of the weakly developed anterior hinge ear. The anterior margin is evenly rounded; the ventral margin is concave; and the posterior margin is obliquely rounded. In the right valve two concavities are present, one at the postero-dorsal angle and the other at the antero-dorsal angle.

The ridges are well developed and broad; there is a well marked anterior zone of reticulation. The ornamentation between the ridges consists of puncta arranged in three rows, or two rows between the ventral ridges. The sub-central plexus is large and prominent.

The inner margin has three broad indentations ; the posterior segment has a greater slope than the median segment.

Three larval stages have been recognized, no. 6, 7, and 8. Ridges are weakly developed, being stronger in the right valve than in the left. In no. 8 all the ridges are present with a similar arrangement to those of the adult ; there is a fine punctation between them. In no. 7 only the more ventral ridges are seen (ridges $4-\mathrm{r} 3$ ), and in no. 6 a few very faint lines can be seen in the postero-ventral region, where there is a slight swelling.

Dimensions:
Length of combined left and right valves:

| Female | $\mathrm{I} \cdot 05 \pm 0.01$ |
| :--- | :--- |
| Male | $\mathrm{I} .15 \pm 0.03$ |


|  | Left valve |  |  |  | Right valve |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | $\frac{1}{2} \mathrm{~W}$ | L | H | L/H |
| Female | I .03 | 0.58 | I 78 | 0.3 I | I .02 | 0.5 I | 2.00 |
| Male | $\mathrm{I} . \mathrm{I} 5$ | 0.58 | I .98 | 0.3 I | $\mathrm{I} . \mathrm{I} 4$ | 0.56 | 2.04 |

Mean length of larval stages:
No. 8, o.88; no. 7, 0.74; no. 6, o.61.
Discussion: This differs from C. tenuistriata tenuistriata (Reuss) in the stronger ornamentation. The ridges are much more pronounced, there are no smooth area in the anterior and posterior regions, and the pitting between the ridges is finer than in C. tenuistriata tenuistriata. See also C. tenuipunctata and C. minipunctata sp. nov.


Fig. 20. Cythevetta tenuistriata (Reuss) ornata subsp. nov.; female right valve; $\times 75$.

## Cytheretta minipunctata sp. nov.

(Pl. 16, figs $\mathrm{I}-3$ )
Derivation of name: Latin-minus, small; punctata, small pits; refers to the ornamentation.

Diagnosis: A species of the superspecies $C$. tenuipunctata with six faint ridges and a finely punctate ornamentation.

Holotype: Io 4028, a female left valve.
Paratype: Io 4029.
Material: 9 valves and carapaces from Cormeilles.
Type locality and horizon: Cormeilles-en-Parisis; Bed no. 44 of Albissin, Couches de Sannois superieur.

Stratigraphical range and distribution: Lower marine Sannoisian of the Paris Basin.

Description: The dorsal and ventral margins of the left valve are sub-parallel and almost straight; a posterior hinge ear is developed; the anterior margin is obliquely rounded towards ventral; the posterior margin is slightly pointed. In the
right valve, the dorsal margin is convex and the ventral margin concave. In both valves there is an elongate dimple in the postero-ventral region.

Ornamentation consists of some 6 faint ridges which are developed in the ventral half of the valve, particularly in the median portion. In between the ridges are 2 or 3 rows of puncta; these also cover a large part of the dorsal area of the valve, where ridges are not developed.

Details of the interior are not clearly seen.
Dimensions:

|  | L | H | $\mathrm{L} / \mathrm{H}$ <br> (Average) | W |
| :---: | :---: | :---: | :---: | :---: |
| Carapaces-Female | $0.94-\mathrm{I} \cdot 00$ | $0.54-0.58$ | $\mathrm{I} \cdot 74$ | 0.48 |
| Male | $\mathrm{I} \cdot \mathrm{IO}-\mathrm{I} \cdot \mathrm{I} 5$ | 0.58 | $\mathrm{I} \cdot 93$ | 0.50 |

DISCUSSION: This shows resemblances to C. tenuistriata tenuistriata in size and shape, but the ornamentation is completely different. The ornamentation is similar to that of $C$. buttensis buttensis subsp. nov, but has fewer ridges and is a different shape.

## Cytheretta buttensis sp. nov.

Derivation of name: French--butte, a hill; refers to the Butte de Cormeille and other buttes of the Paris region where the Sannoisian is found.

Diagnosis: A species of the superspecies $C$. temuipunctata showing great variation in the development of ridges and ornamentation. There are usually rows of small puncta between weak ridges; sometimes reticulate.

Description: The left valve has a posterior hinge ear, almost straight dorsal margin, evenly rounded anterior margin, straight ventral margin, and tapered posterior. The dorsal margin of the right valve is strongly convex, with its greatest height in about the centre. There is a dimple in the postero-ventral region of both valves. Ovate in dorsal view.

The inner margin (Text-fig. 21) is fairly regular ; the posterior and anterior indentations are large, the anterior segment is flat, and the joint median and posterior segments have a gentle slope.

The larval stages are very triangular in shape with a pointed posterior end. The ornamentation is similar to that of the adults.

Three morphotypes have been recognized, which constitute two subspecies (Textfig. 22).

Morphotype $A$ :
This is characterized by the development of longitudinal ridges, usually stronger in the right valve. These follow the basic pattern of the superspecies; no. 7, with a sinuous course, joins no. 9 just before the anterior area of the reticulation; no. 8 joins no. 7 as a faint ridge. Between the ridges are parallel rows of small puncta; there are three rows between the ridges in the median and dorsal part of the valve and two in the ventral part. The sub-central plexus is only weakly developed.

Morphotype B:
Similar to Morphotype A except for the development of faint cross ridges between the longitudinal ones. The surface between the ridges is punctate, as in Morphotype A.

## Morphotype C:

Strong cross ridges are developed between the longitudinal ones, which gives the valve a reticulate appearance. The surface between the ridges is smooth. The sub-central plexus is very weak. An additional ridge is present between no. 2 and 3 .

Cytheretta buttensis buttensis subsp. nov.
(Pl. I5, fig. Io)

1960 Cytheretta tenuistriata Mehrotra (non Reuss) p. 80, pl. I, figs il-I2.
Diagnosis and description : This consists entirely of Morphotype A.
Holotype: Io 4030.
Paratype: Io 403 I .
Material: See fig. 22.
Type locality and horizon : Cormeilles-en-Parisis; Bed no. 46 of Mlle. Albissin, Couches de Sannois Supèrieur.

Stratigraphical range and distribution: Couches de Sannois supèrieur.
Dimensions (Carapace)

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | $0.92 \pm 0.04$ | $0.5 \mathrm{I} \pm 0.02$ | $\mathrm{I} .80 \pm 0.04$ | 0.48 |
| Male | $\mathrm{I} .02 \pm 0.04$ | $0.52 \pm 0.02$ | $\mathrm{I} .95 \pm 0.03$ | 0.45 |

Cytheretta buttensis reticulata subsp. nov.
(Pl. 15, figs I-8; Text-fig. 21)
Derivation of name: Latin-reticulatus, net-lıke; refers to the ornamentation.
Diagnosis and description: Consists predominantly of Morphotype C together with Morphotypes A and B.

Holotype: Io 4032.
Paratypes: Io 4033-8.
Material: See Fig. 22.
Type locality and horizon : Cormeilles-en-Parisis; Bed no. 47 of Mlle. Albissin, Couches de Sannois supèrieur.

Stratigraphical range and distribution: Couches de Sannois supèrieurMarnes à Huîtres infèrieurs.

Dimensions: (Carapace) ;

|  | L | H | L/H | W |
| :--- | :--- | :---: | :---: | :---: |
| Female | $0.85 \pm 0.025$ | $0.48 \pm 0.01$ | $\mathrm{I} .79 \pm 0.03$ | 0.42 |
| Male | $0.97 \pm 0.02$ | $0.50 \pm 0.0 \mathrm{I}$ | $\mathrm{I} .94 \pm 0.03$ | 0.43 |



Fig. 21. Cytheretta buttensis reticulata sp. subsp. nov.; female left valve; $\times 75$.

Discussion: Morphotype A resembles C. bernesis Oertli from the Rupelian of Switzerland; they differ in dorsal outline, as C. bernesis is tapered towards the anterior. The longitudinal ridges are also unequally developed in the latter; ridges no. 3 is strong, while nos. 4,5 and 6 are weak, and they also form a slightly different pattern. C. ramosa sublaevis Triebel from the Chattian Cyrenenmergel of the Mainz Basin is similar, but the longitudinal ridges are very weak and can hardly be seen in the right valve; the surface of the valve is also more uneven, with marked longitudinal swellings in the position of ridges nos. 4 and 9 ; these swellings are much more apparent in C. ramosa ramosa (Lienenklaus).

|  | SAMPLE NUMBER | MORPHOTYPE \% |  |  | Subspecies of C.buttensis |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | A | B | C |  |
| $\cdots$ | 22 (48) | 100 | - | - | buttensis |
| - 山 | 23 (79) | 33 | 19 | 48 |  |
|  | 24 (72) | 23 | 7 | 70 | reticulata |

Fig. 22. Distribution of morphotypes of Cytheretta buttensis sp. nov. from Cormeilles. Note that the stratigraphical sequence has youngest at the bottom.

The stratigraphically arranged series of specimens from the Paris Basin shows certain trends. The earliest species, C. minipunctata sp. nov. and C. buttensis sp. nov. buttensis subsp. nov., have very weakly developed ridges with several rows of puncta between them. In the later species the ridges become stronger and the puncta in between them become larger with fewer rows, as in C. tenuipunctata absoluta and C. temuipunctata lirata. In the latter the ridges are very strong and the pitting is reduced to a single row of large pits.

It is considered that the relationships suggested in Fig. 23 represent a possible phylogeny.

The barrier may be ecological rather than geographical sensu stricto. C. minipunctata, or something like it, is a possible ancestor of $C$. tenuistriata with its two recorded geographical sub-species.

It is interesting to note that in Switzerland the finely punctate species with weak ridges, $C$. variabilis and $C$. bernesis, occur at a stratigraphically lower horizon than C. tenuistriata tenuistriata, as in the Paris Basin. In the Mainz Basin these postulated early forms are not present, possibly because the Sannoisian is poorly exposed, but more likely because they were not present in the area; they have not been found in samples collected nor recorded in the works of Triebel, Stchepinsky and Gramann. In the Chattian of the Mainz Basin there are, however, two finely punctate forms, C. ramosa ramosa (Lienenklaus) and C. ramosa sublaevis (Triebel). The valve of the former has an uneven surface, similar to $C$. variabilis, and both of these are only tentatively included in the superspecies. C. ramosa sublaevis has a much smoother valve with fine punctae between weak ridges.
C. stigmosa Triebel has a similar ridge pattern, but varies in shape and has much larger pitting. The two must be closely related, however.

The L/H ratio of all the female left valves from the Paris Basin were averaged, and gave an answer of $\mathrm{I} 79 \pm 0.04$.


Fig. 23. Suggested relationship between Cytheretta buttensis sp. nov. and Cytheretta tenuipunctata (Bosquet).

This standard deviation compares favourably with that of individual species, so it is concluded that this is a further character to be considered in diagnosing the superspecies.
C. minor (Lienenklaus), C. stigmosa Triebel and C. regularis sp. nov. show similarities to the superspecies C. tenuipunctata (Bosquet) in ornamentation, but differ in shape. C. posticalis Triebel has a similar shape to C. tenuipunctata but has almost no ornamentation.

## Cytheretta minor (Lienenklaus)

(Pl. I6, fig. 6)
1905 Cythereis jurinei (von Munster) var. minor Lienenklaus, p. $3^{2 .}$
1952 Cytheretta minor (Lienenklaus) Triebel, p. 24, pl. 4, figs. 22-3.
Diagnosis: A small species of the genus Cytheretta with smooth dorsal and anterodorsal areas and double rows of puncta between weak ridges.

Material: 25 valves and carapaces from Weinheim (Trift). Io 3704.
Type locality and horizon: Weinheim; Unterer Meeressand.
Stratigraphical range and distribution: Mainz Basin, Unterer Meeressand; Paris Basin, Couches de Sannois supèrieur. Falun de Morigny.

Description : In the left valve there is a posterior hinge ear; the dorsal margin is very slightly convex and the greatest height is about one quarter of the way from the anterior. The anterior margin is obliquely rounded; the ventral margin is almost straight and the posterior margin is slightly tapered. In the right valve the dorsal margin is slightly convex and the ventral margin is concave. A few denticles are present along the anterior margin of the right valve. Ovate in dorsal view.

The dorsal and antero-dorsal regions are smooth, so that ridges no. I and 2 are absent. To the anterior of the sub-central plexus ridges $b$ and $c$ are prominent, but where ridge a would be is a diffuse area of puncta. There is a double row of puncta between the ridges. In most specimens the ridges are merely areas without puncta, but this gap between the double rows of pits is greater than that between the contained single rows. In a few specimens, however, actual ridges are present.

Dimensions: (Carapaces).

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.88 | 0.53 | I.66 | 0.45 |
| Male | 0.85 | 0.50 | I.70 | 0.43 |

Discussion : This could be included in the superspecies due to the similarity of the ridge pattern, even though ridge no. a is absent. The size seems to vary; the dimensions given by Triebel are less than those of the material examined from Weinheim, where it is the commonest Cytheretta species; those from the Paris Basin are in better agreement with Triebel. It shows a great resemblance to C. tenuistriata tenuistriata (Reuss), with which it is associated in the Mainz Basin. It is much smaller, however, and there are no specimens of intermediate size; it has a slightly different shape, and lacks ridge a.

## Cytheretta posticalis Triebel

Diagnosis: A large species of Cytheretta with an elongate shape, sub-parallel dorsal and ventral margins, and prominent posterior hinge ear. It is almost smooth, with a faint ornamentation of ridges and puncta in the posterior and ventral parts of the valve.

## Cytheretta posticalis posticalis Triebel

1905 Cythereis jurinii Lienenklaus (non von Münster), p. 31.
1952 Cytheretta posticalis Triebel, p. 23, pl. 3, figs 18-21.
1956 Cytheretta posticalis Triebel, Oertli, p. 59, pl. 6, figs 160-162.
Type locality and horizon: Welschberg (Mainz Basin), Unterer Meeressand.
Stratigraphical range and horizon: Mainz Basin: Unterer Meeressand, Schleichsand, Cyrenenmergel; Switzerland: Meeressand, Blaue Tone (both Rupelian).

Cytheretta posticalis parisiensis subsp. nov.
(Pl. I8, figs I-4, 6)
Derivation of name: Named after Paris.
Diagnosis: A subspecies of $C$. posticalis showing a large amount of variation in areas of ornamentation.

Holotype: Io 4039.
Paratypes: Io 4040-42.
Material: 22 valves from Auvers-St.-George; 5 from Morigny.
Type locality and horizon: Auvers-St.-George, Stampian.
Stratigraphical range and distribution: Auvers-St.-George, Morigny; Stampian of the Paris Basin.
Description: Sexual dimorphism is pronounced, the males being more elongate. The left valve has a strong posterior hinge ear and a weak anterior one ; this causes the dorsal margin to have an undulating appearance. This is particularly true of the male. The anterior margin is evenly rounded; the ventral margin, almost parallel to the dorsal, is slightly concave in the male and convex in the female. The posterior margin is tapered. In the right valve the dorsal margin is almost straight and the ventral is concave. It is ovate in dorsal view.

The ornamentation varies. Some specimens are completely smooth; some have a few faint double rows of puncta in the ventral portion of the postero-median region; others have a few faint ridges with puncta between in the postero-ventral angle.

The internal features are as for the superspecies $C$. temuipunctata with inner margin similar to C. tenuistriata ornata.

Discussion: C. posticalis posticalis differs only in the ornamentation, which is restricted to a few ridges in the postero-ventral angle. Some specimens of
C. posticalis parisiensis are exactly the same, but the great variation within the sample is taken to indicate subspecific differentiation.
C. klahni Stchepinsky from the Stampian Marnes à Cyrènes of Alsace has ornamentation confined to the median and posterior parts of the valve and consists of double rows of small puncta. In this respect it is similar to some of the specimens of C. posticalis parisiensis. However, the lateral outline has a rhomboidal appearance due to the shape of the posterior margin, which differs from C. posticalis; and in dorsal outline it is more tapered. It is much smaller, but is probably a related species.

Dimensions:

|  | Left valve |  |  | Right valve |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | $\mathrm{L} / \mathrm{H}$ | L | H | $\mathrm{L} / \mathrm{H}$ |
| Female | 0.95 | 0.53 | I .79 | 0.9 I | 0.47 | I .94 |
| Male | I .05 | 0.53 | I .98 | I .03 | 0.49 | $2 . \mathrm{IO}$ |

## Cytheretta headonensis Haskins

(PI. 18, figs II-I4; Text-fig. 24)
1857 Cytherideis colwellensis Jones (pars) p. 49, pl. 14, figs 20a-c.
1870 Cythere ? Jones p. 157 and 159.
1887 Xestoleberis aurantia non Baird, var. Jones and Sherborn, vol. 4, p. 456.
1889 Cytherideis colwellensis Jones, Jones and Sherborn p. 45.
1968 Cytheretta rhenana headonensis, Haskins, p. 167, pl. 3, figs 11-18.
Diagnosis: An unornamented species of Cytheretta with a strongly obliquely rounded anterior margin.
Material: 3 valves from Headon Hill; 16 from Colwell Bay; 17 from Milford; 7 from Whitecliff Bay. Io 4043-7.

Type locality and horizon: Although there are grounds for believing that Headon Hill is the type locality due to etymology, in the type description Whitecliff Bay is quoted; Middle Headon Beds.


Fig. 24. Cytheretta headonensis Haskins; female right valve; $\times 75$

Stratigraphical range and distribution: Middle Headon Beds of Headon Hill, Colwell Bay, Whitecliff Bay, and Milford.

Discussion: This is very similar to C. rhenana Triebel; the left valve of $C$. headonensis has a much more obliquely rounded anterior margin, as well as more anterior radial pore canals ( 34 compared with 27).

Jones figured two different ostracods as his new species Cytherideis colwellensis; all of the material is preserved in the British Museum (Nat. Hist.), No. I 643 ( (13). Pl. 4, fig. I3 of Jones is a species of Neocyprideis, which has now been selected as the lectotype to avoid taxonomic complications, even though the type is a moult stage and thus not very satisfactory; fortunately it is a very common species so that its diagnosis is possible with topotype material of the adult.

Cytheretta vesca sp. nov.
(Pl. I7, figs 8, 9, 12 )
Derivation of name: Latin-vescus, weak, little; refers to the fragile appearance of the carapace.

Diagnosis: A species of Cytheretta with a thin shell and a weak ornamentation consisting of rows of small puncta in the posterior and latero-ventral areas of the carapace.

Holotype: Io 4048, a female left valve.
Paratypes: Io 4049-5I.
Material: 9 valves.
Type locality and horizon: Auvers-St.-George; Stampian.
Stratigraphical range and distribution: So far known only from the type locality.

Description: Sexual dimorphism is distinct, the males being more elongate; sex ratio 1 : r. The left valve has a weak posterior hinge-ear and a convex dorsal margin; the anterior margin is obliquely rounded; the ventral margin is straight; the posterior margin is obliquely rounded, particularly in the female. The ventral margin of the right valve is concave. The carapace is ovate in dorsal view.

The ornamentation consists of a few indistinct rows of very small puncta in the posterior and latero-ventral areas of the carapace.

The hinge of the left valve has a small antero-dorsal lobe, although the corresponding antero-dorsal platform of the right valve is very prominent. The anteroventral lobe is weak; the antero-median tooth is small. The postero-median swelling is prominent in lateral view, but cannot be seen in dorsal view. The anterior tooth of the right valve is large, projecting beyond the dorsal margin ; the posterior tooth is equally prominent in dorsal view, but smaller in lateral view.

The selvage forms the anterior margin; along the ventral margin there is a prominent flange and a wide flange groove; there is a narrow flange groove along the posterior. A list is present. There are some 45 normal pore canals, but the number of radial pore canals could not be determined, nor could the shape of the inner margin.

Dimensions:

|  | Left valve |  |  | Right valve |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | L | H | L/H |
| Female | 0.73 | 0.42 | I .74 | 0.72 | 0.37 | I.95 |
| Male | 0.70 | 0.38 | I .84 | 0.70 | 0.33 | 2.I2 |

Discussion: This differs from C. rhenana in having a weak ornamentation. The ornamentation is much weaker than that of C. stigmosa. It differs from both of these in shape; the dorsal margin of the left valve is more convex and the posterior margin is more obliquely rounded. The carapace of C. vesca is much less massive than these.

## Cytheretta stigmosa Triebel

Diagnosis: A species of the genus Cytheretta with an obliquely rounded anterior margin. The ornamentation consists of longitudinal rows of large pits with ridges in between which become stronger ventrally.

## Cytheretta stigmosa stigmosa Triebel

1952 Cytheretta rhenana stigmosa Triebel, p. 26, pl. 5, figs 28, 29.
Type locality and horizon: Welschberg; Unterer Meeressand.
Stratigraphical range and distribution: Rupelian Meeressand and Schleichsand of the Mainz Basin. Cavelier (1965, determinations by Apostolescu) records it from the Sannoisian of Sannois in the Paris Basin.

Discussion: See $C$. stigmosa gallica sub sp. nov.

## Cytheretta aff. stigmosa stigmosa

(Pl. I6, fig. 8)
Locality and stratigraphical position: Whitecliff Bay, Isle of Wight; Middle Headon, Beds (WBi8). Io 4052.

Discussion : Six poorly preserved specimens, together with one well preserved one, were available for study. No internal characters could be seen. The shape is similar to $C$. stigmosa. The ornamentation is very similar except that the pits are rather smaller and there are more of them per row than in $C$. stigmosa stigmosa. The dorsal and antero-dorsal regions are smooth. It is unknown whether this is a distinct subspecies or the same as that from the Rhine Valley.

## Cytheretta stigmosa gallica subsp. nov.

(Pl. 17, Figs I, 2, 5, IO; Text-fig. 25)
Derivation of name: Latin-Gallica, country of the Gauls.
Diagnosis: A subspecies of $C$. stigmosa in which the ornamentation covers the whole valve and the longitudinal ridges are very narrow.

Holotype: Io 4053, a female left valve.
Paratypes: Io 4054-56.
Material: 44 valves, 4 carapaces.
Type locality and horizon: Auvers-St-George; Stampian.
Stratigraphical range and distribution: So far only known from the type locality.

Description : Sexual dimorphism can be observed, the males being more elongate; sex ratio, $I: I \cdot 5$. The left valve has a posterior hinge ear; the dorsal margin is convex with the greatest height of the valve in line with the sub-central plexus. The anterior margin is obliquely rounded; the ventral margin is almost straight; the posterior margin is obliquely rounded, but only slightly so. In the right valve the ventral margin is concave.

Ridges with pitting between them are present in the ventral part of the valve and would correspond to ridges nos. 7-I3 in the terminology adopted for C. tenuipunctata; ridges b and c can also be seen. In the median and dorsal areas are some seven longitudinal rows of large pits with weak and irregular ridges between them. There is an area of small pits, not arranged in rows, in the antero-dorsal region; to the anterior of the poorly defined sub-central plexus is an area of larger pits, while along the anterior margin there is reticulation.

In the hinge of the left valve the antero-dorsal lobe is slightly swollen; the anteroventral lobe is small; the antero-median tooth is small but prominent; and the postero-median swelling is of equal size and prominence as the antero-median tooth.

The selvage runs close to the anterior and posterior margins so that there is only a very small flange groove present in these regions which is better seen in the right valve. Along the ventral margin of the right valve there is a wide flange groove.

The inner margin has a beak-shaped anterior indentation, prominent ventral, and a high and fairly narrow posterior indentation. The anterior segment is gently rounded, the median is short and curves into the steep posterior indentation. The distribution of pore canals could not be seen.


Fig. 25. Cytheretta stigmosa Triebel gallica subsp. nov.; male left valve; $\times 75$.

Dimensions:

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.75 | 0.47 | I.57 | 0.38 |
| Male | 0.74 | 0.42 | I.76 | 0.36 |

Discussion: C. stigmosa stigmosa has unornamented dorsal and antero-dorsal areas and smaller pits with wider areas between the rows. Thus it differs from the almost reticulate appearance of C. stigmosa gallica. C. minor is rather similar but has double rows of puncta instead of single rows of large pits and unornamented areas as in C. stigmosa stigmosa; its lateral outline is also different. See also C. regularis sp. nov. and C. bullans sp. nov.
C. stigmosa is here regarded as a separate species rather than a subspecies of C. rhenana because the two are found together and should therefore be regarded as distinct species or as varieties or morphotypes of a single species. There is also a lack of intermediaries and the difference cannot be sexual because sexual dimorphism can be recognized with each group. It should be pointed out, however, that small unornamented forms and pitted forms similar to C. rhenana and C. stigmosa are found together not only in the Rhine Valley, but in the Paris Basin, Aquitaine Basin and the Hampshire Basin. They do not always occur in the same sample, but do occur at the same locality and in adjacent horizons. They perhaps inhabited different ecological zones and could represent ecologically separated subspecies. As this is not proven, the evidence still favours them as distinct species.

Cytheretta regularis sp. nov.
(Pl. r7, figs 3, 4, 6, 7; Text-fig. 26)
Derivation of name: Latin-regularis, regular; refers to the smooth and regular lateral outline of the left valve.

Diagnosis: A species of Cytheretta with a straight dorsal margin in the left valve, sub-parallel dorsal and ventral margins, and an evenly rounded posterior margin. Ornamentation consists of longitudinal rows of pits with a smooth antero-dorsal region. Sexual dimorphism is not pronounced.

Holotype: Io 4057.
Paratypes: Io 4058-60.
Material: 12 valves and carapaces from Espibos, 6 from Lesbarritz.
Type locality and horizon: Lesbarritz, Gaas (AGLi); Stampian.
Stratigraphical range and distribution: Lesbarritz and Espibos, Gaas; Stampian.

Description: Sexual dimorphism is not very pronounced, the males being slightly more elongate; sex ratio $x: 2$. The dorsal margin of the left valve is straight with no posterior hinge ear; the anterior margin is slightly obliquely rounded; the ventral margin is almost straight ; and the posterior margin is evenly rounded. In the right valve the dorsal margin is convex and the ventral is concave. The dorsal and ventral margins are almost parallel. In dorsal view the carapace is ovate.

The ornamentation consists of 13 longitudinal rows of pits between narrow ridges. The sub-central plexus is fairly prominent although not appearing so in the electron scanning photographs, and to its anterior are two prominent ridges which slope towards the antero-ventral angle. The anterior and posterior regions are covered by numerous small pits. The extreme antero-dorsal area is smooth.

In the hinge of the left valve the antero-dorsal lobe is small and slightly swollen; the antero-ventral lobe is poorly developed; the antero-median tooth is small and the postero-median swelling is hardly noticeable. In the right valve the anterior tooth is much smaller and globose in shape.

The selvage is very close to the margins of the valve with a flange groove developed along the ventral margin and a small one along the posterior margin. The inner margin has three prominent indentations; the anterior one is rather ill defined in the specimens available, but is narrow; the ventral one is very long and narrow; the posterior one is small. The anterior segment is unevenly rounded; the median segment is short with a gentle curve ; the posterior segment is long with a fairly steep slope. There are some 27 anterior radial pore canals, tending to be grouped into five sets; 35 closely spaced posterior radial pore canals; io ventral radial pore canals; and some 38 normal pore canals, which are not related to the ornamentation except that they mainly open into the pits of the outer surface.

The central muscle scars are in a slight pit with four equal small and circular adductor muscle scars along the posterior edge of the pit and a large frontal muscle scar on the anterior edge. The fulcral point is not very prominent.

Dimensions:

|  | Left valve |  |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | $\mathrm{L} / \mathrm{H}$ | L | H | $\mathrm{L} / \mathrm{H}$ |  |  |
| Female | 0.70 | 0.38 | I .84 | 0.68 | 0.35 | I .94 |  |  |
| Male | 0.70 | 0.37 | I .88 | 0.68 | 0.33 | 2.06 |  |  |

Discussion: This differs from $C$. stigmosa in shape, particularly of the dorsal margin. The ornamentation is very similar to C. stigmosa gallica and also to C. bullans. It differs from the latter in the shape of the anterior margin, in size, and in the constancy of development of the ornamentation. It differs from C. minor in having single rows of large pits instead of double rows of puncta, as well as in shape.


FIG. 26. Cytheretta regularis sp . nov.; male right valve; $\times 75$.

Cytheretta bullans sp, nov.
(Pl. 18, figs 5,7 ; Pl. 22, fig. II)
Derivation of name: Latin-bulla, bubble; refers to the ornamentation which resembles strings of bubbles.

Diagnosis: A species of the genus Cytheretta with parallel dorsal and ventral margins and evenly rounded anterior and posterior margins. Ornamentation consists of longitudinal rows of pits often with a large unornamented anterior region.

Holotype: Io 406 r .
Paratype: Io 4062.
Material: i8 carapaces.
Type locality and horizon: Chateau Romefort, Blaignan; Argile à Algues, Sannoisian.

Stratigraphical range and distribution : Known only from the type locality.
Description: Sexual dimorphism is distinct, the males being more elongate; sex ratio, $1: 2$. The dorsal and ventral margins of the left valve are parallel. The dorsal margin of the left valve is straight without a posterior hinge ear; the anterior margin is evenly rounded; the ventral margin is very slightly concave; the posterior margin is evenly rounded. In dorsal view it is ovate with a tapered anterior end.

The degree of development of the ornamentation varies. There are some thirteen rows of pits with ridges between to the posterior of the ill-defined sub-central plexus. To the anterior are two prominent ridges which slope towards the antero-ventral angle. There is an anterior area of reticulation with small pits in between. The antero-dorsal area is smooth. This unornamented anterior area varies in size; in some specimens the whole anterior area is smooth and in others the ornamentation is restricted to six or seven rows of pits in the postero-median position. It must be emphasized that this is not a form of sexual dimorphism, as might be inferred from Pl. I8, figs 5, 7 .

Internal characters could not be seen.
Dimensions: Carapace

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.85 | 0.48 | I .77 | 0.43 |
| Male | 0.90 | 0.45 | 2.00 | 0.40 |

Discussion : See C. regularis. It differs from C. stigmosa in lateral shape, and from C. minor in having single rows of large pits instead of double rows of puncta, as well as in shape.

## Cytheretta sagri Deltel

Diagnosis: A species of Cytheretta with thirteen longitudinal ridges, often only present in the posterior. The inner margin has a characteristic shape with a depressed median segment markedly separated from the anterior and posterior segments.

Description: Six morphotypes divisible into three subspecies have been recognized; these are described below. The shape and ornamentation vary to a great extent, but the internal structures appear to be constant. Another feature that is constant is the five posterior spines.

The hinge of the left valve has a prominent swollen antero-dorsal lobe; a strong antero-ventral lobe; a large antero-median tooth; a very weak postero-median swelling, and a large posterior socket. In the right valve the anterior tooth is much larger than the posterior one.

The selvage runs very close to the anterior margin; a wide flange groove is present along the ventral margin with a narrow one along the posterior. The inner margin is very characteristic of the species. The anterior and posterior indentations are narrow; the ventral indentation is narrow and ' $V$ '-shaped. The anterior and posterior indentations are semi-circular; the median segment is sharply differentiated from these, lying close to the ventral margin and with a postero-ventral indentation.

There are 25 anterior radial pore canals, 33 posterior, and 14 ventral. The central muscle scars are in a pit; the two lowest adductors are almost joined, and the frontal is inside the pit. The fulcral point is large and prominent.

## Morpholype A:

Sexual dimorphism is pronounced, the males being more elongate. The left valve has a strong posterior hinge ear and a weak anterior one; the dorsal margin between these is symmetrically convex in the female and asymetrically convex in the male with the stcep slope towards the posterior. The anterior margin is slightly obliquely rounded with some nine denticles in the ventral half. The ventral margin of the female is straight, while that of the male is concave. The posterior margin is evenly rounded. The dorsal margin of the right valve has a marked protuberance in the anterior half caused by the high position of the antero-median socket of the hinge; the ventral margin is concave. In dorsal view the female is ovate and tapered towards the anterior; the male is more bullet-shaped.

The ornamentation consists of thirteen longitudinal ridges. In the right valve ridges nos. 4 and 8 are sometimes very strong with a slight depression developed between them. Ridge no. 6 is thin, bifurcating at its anterior end just to the posterior of the sub-central plexus, one part joining no. 5 and the other no. 7. This ridge is always weak in the right valve, but in some left valves it is strong, stronger in fact than no. 7 , so that it appears that no. 7 joins it instead of the other way round. To the anterior of the weak sub-central plexus are four prominent ridges sloping towards the antero-ventral angle. Faint cross-ridges and meandriform punctation are developed between the longitudinal ridges (see Pl. 2I, fig. 5 for meandriform punctation).

## Morphotype B:

This differs slightly from Morphotype A in shape; it has a more rectangular outline due to the evenly rounded anterior margin, and in dorsal view it is ovate, not tapered. The whole of the anterior margin is denticulate with some twelve denticles. The
ornamentation is similar to that of Morphotype A, except that there is a smooth area of varying extent in the antero-dorsal region. The internal details could not be seen.

## Morphotype C:

The female left valve has no anterior hinge ear, so the antero-dorsal angle is a smooth curve, unlike Morphotypes A and B. In dorsal view it is ovate. The ornamentation is restricted to the posterior part of the valve where $9-\mathrm{I} 3$ ridges can be seen. Ridge no. 6 is clearly recognizable and of equal strength to the other ridges. No internal details could be seen.

## Morphotype D:

This is similar in shape to Morphotype C and the ornamentation is also restricted to the posterior. It differs in the inequality of the ridges; no. 6 in particular is weaker.

## Morphotype E:

The female left valve has no anterior hinge ear, but the lateral outline of the carapace differs from Morphotypes C and D in being almost triangular with a very prominent posterior hinge ear. The carapace is unornamented over a large anterior and antero-dorsal area; longitudinal ridges are present over the remaining surface with a very fine meandriform punctation between them. Ridge no. 6 is very weakly developed. This differs from Morphotype B in shape and in having a much weaker ornamentation without the cross-ridges present between the longitudinal ridges.

## Morphotype F:

This is very similar to Morphotype E, except that the ornamentation is restricted to the posterior half of the valve. Ridge no. 6 is very faint and thread-like, leaving a prominent gap between nos. 5 and 7 ; in this respect it differs from Morphotype C.

## Cytheretta sagri sagri Deltel

(Pl. I9, figs. I-4; text-fig. 28)
1964 Cytheretta sagri Deltel, p. 156, pl. 3, figs 56-57.
Diagnosis and description: A subspecies of $C$. sagri consisting predominantly of Morphotype A with Morphotype D.
The last two larval stages have been recognized. The ornamentation in no. 8 consists of two prominent ridges, nos. 4 and 8 of the adult, with the other ridges of the adult stage weakly developed. Cross-ridges are sometimes present; puncta are present between the ridges. There are four posterior spines and eleven anterior denticles, each bearing one of the eleven anterior pore canals. In the seventh larval stage the two ridges nos. 4 and 8 are present. There are seven anterior radial pore canals and denticles and two posterior spines.

Material: See fig. 27. Io 4063-6.
Type locality and horizon: Lesbarritz, Gaas; Stampian.
Stratigraphical Range and distribution: Stampian of Gaas (Lesbarritz Espibos) and Bastennes-Gaujacq, Aquitaine Basin.

Dimensions:
Morphotype A

|  | Left valve |  |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | $\mathrm{L} / \mathrm{H}$ | $\frac{1}{2} \mathrm{~W}$ | L | H | $\mathrm{L} / \mathrm{H}$ |  |
| Female | 0.84 | 0.45 | I .87 | 0.22 | 0.84 | 0.42 | 2.00 |  |
| Male | 0.90 | 0.47 | I .9 I | 0.24 | 0.90 | 0.43 | 2.09 |  |

Morphotype $D$ (Carapace):

|  | L | H | L/H | W |
| :---: | :---: | :---: | :---: | :---: |
| Female | 0.92 | 0.53 | I.74 | 0.46 |


| MORPHOTYPE SAMPLE | A | B | C | D | E | F | Subspecies of C. sagri |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| AGE 1 | 12 |  |  |  |  |  | sagri |
| AGE 2 | 21 |  |  |  |  |  |  |
| AGL 1 | 1 |  |  | 4 |  |  |  |
| S493 | 8 | 24 | 52 |  |  |  | inconstans |
| RO 264 |  |  |  | 4 | 3 |  | martini |
| RO 266 |  |  |  |  |  | 1 |  |
| RO 268 |  |  |  |  | 1 | 5 |  |
| RO 269 |  |  |  |  | 22 | 8 |  |
| RO 270 |  |  |  |  |  | 21 |  |
| RO 271 |  |  |  | 1 | 4 | 6 |  |

Fig. 27. Distribution of Morphotypes of Cytheretta sagri Deltel.
Cytheretta sagri inconstans subsp. nov.
(Pl. 19, figs 5-7, 9)
Derivation of name: Latin-inconstans, the opposite of standing firm, or inconstant; refers to the great variation of shape and ornamentation.

Diagnosis and description: A subspecies of $C$. sagri showing variation in shape and ornamentation. The latter consists of thirteen longitudinal ridges which in some specimens cover the whole valve and in others only the posterior region. It consists predominantly of Morphotype C with A and B.

Holotype: Io 4067, a female left valve.
Paratypes: Io 4068-70.
Material: See fig. 27.
Type locality and horizon: Chateau Romefort, Blaignan; Argiles à Algues, Sannoisian.

Stratigraphical range and distribution: So far only known from the type locality.

Dimensions: Carapaces

|  | Morphotype B |  |  | Morphotype C |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | W | L | H | L/H | W |
| Female | 0.78 | 0.43 | I.8I | 0.38 | 0.92 | 0.53 | I.74 | 0.47 |
| Male | 0.83 | 0.43 | I.93 | 0.39 | 0.95 | 0.47 | 2.02 | 0.42 |

Cytheretta sagri martini subsp. nov.
(Pl. 20, figs $\mathrm{I}-4$ )
Derivation of name: From the Phare St. Martin, Biarritz.
Diagnosis and description: A subspecies of $C$. sagri of a triangular shape in lateral view and with a weak ornamentation. It consists of Morphotypes D, E and F, particularly the last two.

Holotype: Io 407x, a female left valve.
Paratypes: Io 4072-6.
Material: See fig. 27.


Fig. 28. Cythevetta sagvi Deltel; female left valve. $\times 75$

Type locality and horizon: Couches du Phare, Biarritz (RO 270); Stampian.
Stratigraphical range and distribution: So far only known from the type locality.
Dimensions:
Morphotype E

|  | Left valve |  |  | Right valve |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | L | H | L/H |
| Female | 0.83 | 0.45 | I .84 | 0.8 I | 0.40 | 2.03 |
| Male | 0.86 | 0.45 | I .9 I | 0.90 | 0.43 | 2.09 |

Morphotype F (Carapace):

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.85 | 0.47 | I.8I | 0.39 |
| Male | 0.87 | 0.45 | I.93 | 0.40 |

Discussion: C. sagri Deltel may be the form described by Reuss (1869) as Cythera multinervis sp. nov. (p. 482, pl. 6, fig. 2).

The Oligocene of Aquitaine contains a group of closely related species: C. sagri Deltel, C. gibberis sp. nov., C. minipustulosa sp. nov., C. postornata sp. nov., and C. samothracia Deltel; C. perita Deltel from the Upper Eocene is perhaps related to this group.
C. sagri (Morphotype A), C. minipustulosa and C. samothracia have an unusual meandriform punctation between the longitudinal ridges, but the pattern of the ridges differs amongst the three species. C. sagri (Morphotypes C, D and G), C. gibberis, C. perita and C. postornata are similar in that the ornamentation is restricted to the posterior. C. gibberis differs in the unusual shape of the right valve with its dorsal "hump"; C. perita differs in shape in having only four posterior spines and in the shape of the inner margin; C. postornata also differs in shape and in ornamentation, which consists of six sulca, one of which reaches to the centre of the carapace.
C. tenuipuncta (Bosquet), C. tenuistriata (Reuss) and C. buttensis sp. nov. reticulata subsp. nov. are similar to C. sagri (Morphotype A), but have a different ridge pattern and lack the characteristic meandriform punctation. C. buttensis reticulata has cross-ridges similar to C. sagri (Morphotypes A and B), but differs by the features already mentioned. C. posticalis Triebel has the ornamentation restricted to the posterior, but this is much weaker than the ornamentation of C. sagri (Morphotypes $\mathrm{C}, \mathrm{D}$ and G$)$ and is developed in a more ventral position; it also differs in shape.

## Cytheretta samothracia Deltel

## (Pl. 2I, figs 5, 6, 8)

1964 Cytheretta samothracia Deltel, p. 158, pl. 3, figs 58-60.
Diagnosis and description: Sexual dimorphism is pronounced; the female carapace is quadrate in lateral view, the male is rectangular. There are five prominent posterior spines. Ornamentation consists of eleven longitudinal ridges, including
two prominent parallel ridges in the median part of the valve and two in the dorsal part. Between the ridges is a meandriform punctation and a faint reticulation.

Material: 36 valves and carapaces from Biarritz. Io 4077-79.
Type locality: Bastennes-Gaujacq; Stampian.
Stratigraphical range and distribution: Bastennes-Gaujacq, Lourquen; Stampian. Couches du Phare, Biarritz; Stampian.

Dimensions:

|  | Left valve |  |  | Right valve |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | $\mathrm{L} / \mathrm{H}$ | L | H | $\mathrm{L} / \mathrm{H}$ |
| Female | 0.95 | 0.56 | I .70 | 0.95 | 0.49 | I .94 |
| Male | I .04 | 0.55 | I .89 | I .00 | 0.50 | 2.00 |

DISCUSSION: In shape and ornamentation this is easily distinguished from other species of Cytheretta. See also C. sagri and C. minipustulosa.

Cytheretta minipustulosa sp. nov.
(Pl. 2I, figs I-4; Text-fig. 29)
Derivation of name: Latin-mini, small; pustulosa, full of pimples; refers to the ornamentation between the longitudinal ridges.

Diagnosis: A species of Cytheretta with eleven longitudinal ridges, four of which join in the anterior to form two concentric ovals open towards the posterior. Between the ridges are faint cross-ridges and a meandriform punctation.

Holotype: Io 4080, a male right valve.
Paratypes: Io $408 \mathrm{I}-83$.
Material: I5 valves and carapaces from Biarritz; I valve from Gaas.
Type locality and horizon: Biarritz; Couches du Phare superieur.
Stratigraphical range and distribution: Couches du Phare, Biarritz (Stampian); Espibos (Gaas), Stampian.

Description: In lateral view the carapace is rectangular. Sexual dimorphism is not very pronounced, the males being more elongate. The left valve has a posterior


Fig. 29. Cytheretta minipustulosa; male right valve; $\times 75$.
hinge ear and a weak anterior one; the dorsal margin between is slightly convex. The anterior margin is almost evenly rounded. The ventral margin is slightly concave, particularly in the male. The posterior margin is evenly rounded with five spines. In the right valve the dorsal margin has a protuberance due to the high position of the antero-median socket. The ventral margin is concave; the posterior has five spines, and there is a marked concavity in the postero-dorsal angle. In dorsal view the female is tapered, while the male has more or less parallel sides.

Ornamentation consists of eleven longitudinal ridges. Ridges nos. 2 and 6, and nos. 3 and 5 join in the anterior and form two concentric ovals, open towards the posterior. Ridge no. 4, which is weak, runs down the centre. Nos. 5 and 6 join towards the posterior. Between the longitudinal ridges are faint cross-ridges and a meandriform punctation. There is no sub-central plexus.

The hinge of the left valve has a swollen antero-dorsal lobe; a strong antero-ventral lobe ; a deep anterior socket; a small antero-median tooth; and a weak postero-median swelling. In the right valve the anterior tooth is large and pointed; the posterior tooth is small.

The selvage is strong. It runs close to the anterior margin but a small flange groove is present; the flange groove along the ventral margin is not large. The selvage is very strong in the posterior forming a projecting ridge, to the posterior of which is the flange groove. The latter has more the appearance of a platform; the flange is weak.

The inner margin has a characteristic shape. The anterior and posterior segments are narrow and deep; the ventral indentation is small, but because of the shape of the posterior segment it is very prominent. The anterior segment is semi-circular; the median segment is small and overshadowed by the steeply curved posterior segment, which sweeps up close to the dorsal margin.
The two lower adductor muscle scars touch; the third is elongate; the topmost one is triangular. The fulcrum is not very prominent. No pore canals could be seen.

Dimensions:

|  | Left valve |  |  |  | Right valve |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | $\mathrm{L} / \mathrm{H}$ | W | L | H | $\mathrm{L} / \mathrm{H}$ |
| Female | 0.88 | 0.48 | I .83 | - | 0.98 | 0.48 | 2.04 |
| Male | I .00 | 0.48 | 2.08 | 0.40 | I .09 | 0.50 | $2 . \mathrm{I} 8$ |

Discussion: This differs from C. sagri Deltel by the ridges which form two concentric ovals open towards the posterior, in its elongate shape, and in the shape of the inner margin. It differs from C. samothracia Deltel in lacking the two sets of paired ridges, as well as in its more elongate shape.

Cytheretta gibberis sp. nov.

$$
\text { (Pl. } 16 \text {, figs 9, } 10 \text {; Pl. } 19 \text {, figs } 10 \text { ) }
$$

Derivation of name: Latin-gibberis, hump on the back; refers to the shape of the female right valve.

Diagnosis: A species of Cytheretta in which the right valve of the female is very high in the posterior. Ornamentation is restricted to the posterior and consists of twelve radial sulca, the central one being longer than the others.

Holotype: Io 4084, a female right valve.
Paratypes: Io 4085-86.
Material: 9 valves and carapaces.
Type locality and horizon: Couches du Phare superieur (RO 27I), Biarritz.
Stratigraphical range and distribution: So far only known from the type locality.

Description : Sexual dimorphism is distinct, particularly in the right valve. The left valve has a weak posterior hinge ear, in front of which is a slight concavity; the remainder of the dorsal margin is convex. The anterior margin is obliquely rounded; the ventral margin is straight; the posterior margin is evenly rounded with a few small spines. The right valve of the female has a very high posterior dorsal margin, which over-reaches the left valve in the position of the concavity adjacent to the hinge ear. The dorsal margin slopes steeply to the position of the anterior tooth, in front of which is a concavity with the antero-dorsal platform of the hinge. The anterior margin is evenly rounded; the ventral margin is straight. The ventral part of the posterior margin bears some four spines, although the exact number could not be determined; in the dorsal part there is a large concavity. The right valve of the male is not so high posteriorly and has a concave ventral margin. In dorsal view the carapace is ovate.

The ornamentation is restricted to the posterior and consists of some eleven short, radiating sulca with a long central one which reaches to the central region of the carapace. There is a slight postero-ventral depression in the right valve.

Owing to the poor preservation of the material, the internal features could not be completely observed. The hinge of the left valve has a strong antero-dorsal lobe and a prominent antero-median tooth. The right valve has a large antero-dorsal platform and a large anterior tooth; the posterior tooth is fairly small and lies along the postero-dorsal concavity, almost at right angles to the dorsal margin.

The selvage is prominent with a wide flange groove along the anterior, ventral and posterior of the right valve. A weak list is present in the anterior and postero-ventral regions. The inner margin could not be clearly seen; the anterior and posterior indentations are deep and narrow; and the anterior segment is short and semicircular.

Dimensions:

|  | Carapace |  |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | W | L | H/H |  |  |
| Female | 0.86 | 0.52 | I .65 | 0.43 | 0.88 | 0.48 | I .83 |  |
| Male | - | - | - | - | 0.92 | 0.47 | I .96 |  |

Discussion: The shape of the female right valve distinguishes this form from all other Cytheretta spp. in which the ornamentation is restricted to the posterior.

Cytheretta postornata sp. nov.
(Pl. 20, figs 5-8; Pl. 22, fig. I2)
Derivation of name: Latin-post, posterior; ornata, ornament; refers to the ornamentation which is restricted to the posterior.

Diagnosis: A species of Cytheretta in which the ornamentation is restricted to the posterior. This consists of $6-8$ prominent sulca, one of which reaches to the centre of the carapace.

Holotype: Io 4087, a female left valve.
Paratype Io 4088.
Material: io carapaces.
Type locality and horizon: Biarritz; Couches de l'Atalaye (RO 264).
Stratigraphical range and distribution: So far only known from the type locality.
Description: Sexual dimorphism is not very strong. The dorsal margin of the left valve is strongly convex, less so in the right valve. The anterior margin is evenly rounded; the ventral margin is straight in the left valve, slightly concave in the right. The posterior margin is obliquely rounded and has five spines.

Ornamentation is restricted to the posterior half of the carapace and consists of some $6-8$ sulca. These are mainly short, except for the central one which reaches to the centre of the carapace. Within this long sulcus is a fine threadlike ridge. No internal details could be seen.

Dimensions: Carapaces

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.83 | 0.49 | I.69 | 0.43 |
| Male | 0.84 | 0.47 | I.79 | 0.42 |

Discussion: This is similar to C. sagri Deltel (Morphotypes C, D and F), but differs from these in L/H ratio as well as ornamentation. C. posticalis Triebel has a completely different shape; C. perita Deltel differs in shape, L/H ratio, ornamentation, and has only four posterior spines.

## Cytheretta perita Deltel

> (Pl. I9, fig. 8)

1964 Cytheretta perita Deltel, p. 155, pl. 3, figs 53-55.
Diagnosis and description: The female is triangular in lateral view. There are some eight anterior denticles and four posterior spines. Ornamentation is restricted to the posterior, where there are six short ridges.

Material: io valves and carapace from Lespontes. Io 4089.
Type locality: Coupe de Lespontes, Peyrehorade; Bartonian.

Stratigraphical range and distribution: Coupe de Lespontes (Moulin de Basat; Ferme Le Vigneau).

Dimensions: Carapace

|  | L | H | L/H | W |
| :---: | :---: | :---: | :---: | :---: |
| Female | 0.8 I | 0.43 | I.88 | 0.35 |

Discussion: This differs from C. posticalis Triebel in shape, size, inner margin, and in having stronger posterior ridges. See also C. postornata sp. nov.

## Cytheretta sculpta Ducasse

(Pl. 20, figs 9, Io)

1964 Cytheretta sculpta Ducasse, p. 225, pl. I, figs 2-4.
Diagnosis: A species of Cytheretta with a prominent anterior hinge ear in the left valve. The ornamentation consists of eleven longitudinal ridges with faint crossridges between them.
Material: 9 carapaces. Io 4090-91, Argiles à Algues, Blaignan.
Type locality and horizon: Villeneuve-de-Blaye, Eocène supèrieur.
Stratigraphical range and distribution: Upper Eocene and Sannoisian of the Bordeaux region.

Description: Sexual dimorphism is distinct, the males being more elongate. The dorsal margin of the left valve is slightly convex with a prominent anterior hinge ear. The anterior margin is obliquely rounded; the ventral margin is slightly concave; the posterior margin is evenly rounded. The right valve has a more typical Cytheretta shape due to the lack of the anterior hinge ear. There are some twelve denticles along the whole of the anterior margin and four spines along the posterior margin; these are present in both valves. The carapace is tapered towards the anterior end in clorsal view.

The ornamentation consists of eleven longitudinal ridges; nos. 2, 4, 7 and io run the whole length of the carapace; no. I forms the dorsal margin and in the left valve curves sharply downwards by the hinge ear to join no. 2. No. 3 is faint; no. 5 joins no. 4 just before the anterior margin; no. 6 is faint; no. 9 joins no. 8 in the centre. Another ridge is present just below the hinge ear of the left valve. There is a strong anterior marginal rim. Between the ridges are faint cross-ridges. There is no subcentral plexus.
No internal features could be seen. The antero-dorsal lobe of the hinge is very strong.

Dimensions: Carapaces

|  | L | R | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.70 | 0.40 | I.75 | 0.33 |
| Male | 0.73 | 0.38 | I.92 | 0.33 |

Discussion: The ornamentation is unlike that of any other described species of Cytheretta.

## Cytheretta sp. A

(Pl. 6, fig. II)

Material: i carapace. Io 4092.
Locality and horizon: Moiselles; Sables de Beauchamp.
Dimensions:
Left valve, male: L, o.74; H, o.39; L/H, I•9o.
Discussion: This is very similar to C. ruelensis sp. nov.; the ridge pattern is the same, but the ridges are all of about equal strength. This is probably an individual of a species ancestral to C. ruelensis.

> Cytheretta sp. B
(Pl. 9, fig. I2)
Material: 2 broken right valves, 2 distorted carapaces. Io 4093.
Locality and horizon: Biarritz: Couches à Pentacrinus de la Côte des Basques ( RO 254 ; RO 255); Couches des Bains ( $\mathrm{RO}_{25}$ ).
Description: This has a posterior hinge ear in the left valve and four posterior spines. The ornamentation consists of eleven longitudinal ridges, one of which forms the dorsal margin; ridge no. 6 is short, not reaching to the anterior half of the valve. There is a strong anterior marginal rim and a wide anterior area of reticulation. A weak reticulation is present between the longitudinal ridges.

Dimensions:
Right valve: L, 0.75 ; H, 0.39; L/H, I. 92 .
Discussion: This is of interest as the only Cytheretta sp. found in the Couches à Pentacrinus. There are no other species with which it can be compared.

> Cytheretta sp. C
(Pl. 3, fig. 1o)
Material: I right valve, $\mathrm{L}, 0.70$.
Locality and horizon: Sables d'Auvers, Auvers-sur-Oise.
Discussion: The ornamentation of this valve is very similar to that of C. bambruggensis Keij, but it differs from the latter in having its greatest height situated more to the posterior. The specimen was unfortunately destroyed while being photographed with the electron scanning microscope, but is left here for the record.

Genus FLEXUS Neviani 1928
1928 Flexus, Neviani, p. 26.
1958 Eucytheretta Puri, p. 188.
Type species: Cythere plicata von Munster.

Diagnosis: Similar to Cytheretta but with the development of three prominent longitudinal ridges. Ornamentation between the ridges varies. The carapace tends to be more elongate than Cytheretta.

Discussion: See Introduction.

## Flexus plicatus (von Munster)

(Pl. 22, fig. I)
1830 Cythere plicata von Munster, p. 63.
1838 Cythere plicata von Munster, Roemer, p. 518, pl. 6, fig. 26.
1850 Cypridina plicata (von Munster), Ruess, p. 83, pl. 10, fig. 2 I.
1896 Cythere plicata von Munster, Lienenklaus, p. 141.
1952 Cytheretta plicata (von Munster), Triebel, p. 28, pl. 5, figs 34-35.
1956 Cytheretta plicata (von Munster), Oertli, p. 65, pl. 8, fig. 194.
1958 Eucytheretta plicata (von Munster), Puri, p. 188, pl. 3, figs 1-6.
Type locality and horizon: Astrup, near Osnabruck; Upper Oligocene.
Material: 2 carapaces from Astrup. Io 4094.
Stratigraphical range and distribution: $F$. plicatus has been recorded from a great variety of localities and horizons. Authenticated occurrences however seem to be restricted to the Upper Oligocene of Astrup and Doberg.

Discussion: This occurs together with a form resembling F. concinnus (Triebel); samples from the Upper Oligocene of Bühl near Weimer (Kassel) contain only the latter. This is the form figured and described by Speyer (1863, pl. 4, fig. 2) and mentioned by Lienenklaus ( 1894, p. 198).

## Flexus concinnus (Triebel)

$$
\text { (Pl. 22, figs } 2,3,5 \text { ) }
$$

1852 Cythere plicata Bosquet (pars) (non von Münster), p. 60 , pl. 2, fig. 13.
1895 Cythere plicata Lienenklaus (non von Münster), p. 17.
1905 Cythereis flicata Lienenklaus (non von Münster), p. 37, 64.
1952 Cytheretta concinna Triebel, p. 27, pl. 5, figs 31-33.
1957 Cytheretta concinna Keij, p. r32, pl. ro, fig. 6.
Material: Alzey: io valves; Auvers-St-George: 3. Io 4095-97.
Type locality and horizon: Welschberg; Unterer Meeressand.
Stratigraphical range and distribution: Unterer Meeressand of the Mainz Basin; Stampian of Jeurre, Auvers-St.-George, and Morigny in the Paris Basin; Sables de Berg and Argiles à N. comta, Belgium (Sables de Wemmel and Argiles d'Asche, Belgium ?).

## Flexus gutzwilleri (Oertli)

(Pl. 22, fig. 4)
1956 Cytheretta gutzwilleri Oertli, p. 64, pl. 8, figs 189-192.
Material: 3I valves and carapaces from the topmost Couches du Phare (RO 270, 27I). Io 4098-99.

Type locality and horizon: Therwil (near Basel); Cyrenenmergel (Lower Chattian).

Stratigraphical range and distribution: Lower Chattian of Therwil; Couches du Phare, Biarritz.

Flexus solentensis sp. nov.
Derivation of name: After the Solent.
Diagnosis: A small species of the genus Flexus with a thick anterior marginal rim and thick longitudinal ridges.

Two subspecies have been recognized.
Flexus solentensis solentensis subsp. nov.
(Pl. 23, figs 7-10; Text-fig. 30)
1957 Cytheretta gracilicosta Keij (non Reuss), p. 135, pl. 10, fig. 5.
1968 Cytheretta gracilicosta Haskins (non Reuss), p. 166, pl. 3, figs 1 -io.
Holotype: Io 4100, a female left valve.
Paratypes: Io 4ioi-2.
Material: Barton: EBA 1 (Bed F), 4 valves; EHC 2 (Bed D), 2 carapaces. Alum Bay: Middle Barton Beds, 5 valves and carapaces.

Type locality and horizon: Barton; Middle Barton Beds, Bed F.
Stratigraphical range and distribution: Middle Barton Beds of Barton and Alum Bay.

Diagnosis and description: Sexual dimorphism is distinct; sex ratio, I:3 The left valve has a strong posterior hinge ear and a very weak anterior one; the


Fig. 30. Flexus solentensis solentensis; female left valve; $\times 75$.
dorsal margin is convex. The anterior margin is almost evenly rounded; the ventral margin is concave, particularly in the right valve. The posterior margin is obliquely rounded. In dorsal view all three ridges can be seen, giving the carapace a tapered appearance with the apex at the anterior.

Ornamentation consists of three longitudinal ridges which end against a thick anterior marginal rim. The dorsal ridge forms the dorsal margin between the two hinge ears, curving downwards just to the posterior of the anterior hinge ear. The median ridge is roughly parallel to the dorsal ridge, but with a less accentuated course. The ventral ridge is almost straight. At the posterior the ventral ridge joins the median one and this remaining thin ridge then joins the thin posterior part of the dorsal ridge. Between the ridges is a coarse reticulation of irregular cross-ridges.

The hinge of the left valve has a small swollen, but very prominent, antero-dorsal lobe; the antero-ventral lobe is small; the antero-median tooth is large and the postero-median swelling is almost as big. In the right valve the anterior margin is pointed and the posterior tooth is almost equal in size. The inner margin does not appear to have a very well developed anterior indentation; the ventral and posterior indentations are narrow and deep. The median and posterior segments form a continuous steep curve, going a long way towards the dorsal margin.

There are 24 anterior, 22 posterior and 20 ventral radial pore canals. The selvage is prominent; there is a flange groove along the anterior, posterior and ventral margins; a list is developed in the antero-ventral and postero-ventral areas.

Dimensions:

|  | Left valve |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | W | L | H | L/H |
| Female | 0.52 | 0.3 I | I .68 | 0.25 | 0.5 I | 0.27 | I .89 |
| Male | 0.54 | 0.28 | I .93 | - | - | - | - |

Flexus solentensis congestus subsp. nov.

$$
\text { (Pl. 23, figs } I \mathrm{I}-\mathrm{I} 5 \text { ) }
$$

Derivation of name: Latin-congestus, dense, thick; refers to the longitudinal ridges.

Holotype: Io 4IO3, a female left valve.
Paratypes: Io 4104-5.
Material: EBA 4, 7 valves and carapaces ( 5 females, 2 males).
Type locality and horizon: Barton; Upper Barton Beds (Chama Bed, H).
Stratigraphical range and distribution: So far only known from the type locality and horizon.

DiAgnosis and description: Shape and internal features are as for the nominate subspecies. The ornamentation consists of three very thick ridges which merge into a thick anterior marginal rim. The ridges are thicker than the intervening areas; the latter have a fine, uneven reticulation.

Dimensions:

|  | Left valve |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | L/H | W | L | H | L/H |
| Female | 0.5 I | 0.30 | I 7 O | 0.24 | 0.5 I | 0.25 | 2.04 |
| Male | 0.54 | 0.29 | I .86 | 0.25 | - | - | - |

Discussion: The oldest specimens of $F$. solentensis show similarities to $F$. ludensis sp. nov. in shape, size and ornamentation. In detail, however, the ridges are thicker and the reticulation between them consists of cross-ridges rather than the uneven reticulation of $F$. ludensis. They are quite probably related species however. In younger beds the ridges thicken until in the Upper Barton Beds the end member of the series is met with and is here distinguished as a separate subspecies, $F$. solentensis congestus. The remainder of the Barton Clay has not yielded any ostracods. The overlying Brockenhurst Beds contain a form of $F$. ludensis which must have migrated into the area with the Headon Beds transgression.
$F$. gracilicostuts (Reuss) shows similarities to $F$. solentensis and $F$. ludensis, but has much finer ridges and a smaller and more even reticulation between them. In dorsal view it is more ovate and the three ridges do not stand out as in $F$. solentensis and $F$. ludensis. F. gracilicostus is also much larger.

Flexus ludensis sp. nov.
(Pl. 23, figs $\mathrm{I}-6, \mathrm{I} 6$ )
Derivation of name: After the Marnes à P. ludensis in which it is found.
Diagnosis: A small species of the genus Flexus with thick longitudinal ridges; at the posterior the dorsal and ventral ridges join the median one; at the anterior the ridges join a strong marginal rim. Between the ridges is an uneven reticulation. At the posterior are three small spines.

Holotype: Io 4io6, a female left valve.
Paratypes: Io 4107-12.
Material: Verzy: PVY 2, 8 valves and carapaces; PVY 4, 22. Chavençon: PCC 2, 9 valves and carapaces. Whitecliff Bay: EWB(A), 2 valves and carapaces; EWB(B), 3 ; EWB 19, 2 ; EWB 22, I. Headon Hill: EHH 42, 4 valves and carapaces.

Type locality and horizon: Verzy; Marnes à $P$. ludensis.
Stratigraphical range and distribution: Marnes à P. ludensis of Verzy and Chavençon. Brockenhurst Beds, Whitecliff Bay ; Middle Headon Beds, Headon Hill, Whitecliff Bay.

Description: Sexual dimorphism is pronounced; sex ratio, I $: 2 \cdot 5$. The left valve has a strong posterior hinge ear and a weak anterior one; the dorsal margin is convex. The anterior margin is almost evenly rounded with a few marginal denticles in the ventral portion. The ventral margin is straight in the anterior half, curving round into the posterior margin in the posterior half. The posterior margin is obliquely rounded and has three small spines in the median portion. The right valve
has a concave ventral margin. In dorsal view all three ridges can be clearly seen, giving the carapace a tapered appearance with the apex at the anterior.

Ornamentation consists of three strong, prominent longitudinal ridges which end against a strong anterior marginal rim. The dorsal ridge forms the dorsal margin between the two hinge ears; it curves sharply downwards just to the posterior of the anterior hinge ear. The median ridge is slightly sinuous, running roughly parallel to the dorsal ridge but with a less accentuated course; it is very faint in the extreme posterior, but can be traced right to the margin, just before which it bifurcates. The ventral ridge is almost straight, curving upwards just before reaching the anterior marginal rim. All the ridges are faint at the posterior and tend to disappear amongst the reticulation, but the dorsal and ventral ridges appear to join the median ridge. The anterior marginal rim is particularly strong in the right valve. Between the ridges is an uneven reticulation; there is a particularly prominent "ridge" running between the median and dorsal ridges just to the posterior of centre. The specimens from the Headon Beds lack this "ridge". The area between the dorsal ridge and the antero-dorsal angle is almost smooth.

The hinge of the left valve has a swollen antero-dorsal lobe, prominent anteroventral lobe, large antero-median tooth and a small postero-median swelling. In the right valve the posterior and anterior teeth are about equal in size and rather small. The selvage is prominent, with a small anterior and posterior flange groove and wide ventral one; the flange is particularly prominent along the anterior margin. A list is strongly developed in the antero-ventral and postero-ventral regions. No other internal details could be clearly seen.

Dimensions:

|  | Left valve |  |  |  | Right valve |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | L | H | W/H | W | L | H | L/H |  |
| Female | 0.50 | 0.30 | I .67 | 0.23 | 0.5 I | 0.26 | I .96 |  |
| Male | 0.52 | 0.28 | I .86 | 0.24 | 0.5 I | 0.25 | 2.04 |  |

Discussion: The specimens from the Headon Beds are slightly different from the Ludian ones, particularly with the reticulation between the ridges. The similarities are so strong, however, that it was thought unjustifiable to separate them. See also $F$. solentensis sp. nov.

Flexus lenijugum sp. nov.
(Pl. 21, figs 7, 9; Pl. 22, figs 9, 10)
Derivation of name: Latin-lenis, smooth; jugum, ridge. Refers to the ornamentation.

Diagnosis: A species of Cytheretta with an almost straight posterior margin bearing four spines; apart from the longitudinal ridges the carapace is smooth.

Holotype: Io 4II3, a female left valve.
Paratype: Io 4 II4.
Material: 8 carapaces.

Type locality and horizon: Chateau Romefort, Blaignan; Argiles à algues.
Stratigraphical range and distribution: So far only known from the type locality.

Description: Sexual dimorphism can be discerned, but it is not very prominent. There are anterior and posterior hinge ears in the left valve; the dorsal margin is evenly rounded; the ventral margin is slightly concave in the left valve and strongly so in the right; the posterior margin is almost straight and has four spines. It is tapered towards the anterior in dorsal view.
The ornamentation consists principally of three longitudinal ridges. The dorsal ridge forms the dorsal margin; in the right valve it is continuous with the anterior margin rim; in the left, it ends beneath the anterior hinge ear. The median ridge is short and has another weak ridge above it in the posterior. The ventral ridge is strong, joining the anterior marginal rim and, at the posterior, the weak ridge above the median ridge. The anterior marginal rim is strong, running from the anterior hinge ear to the ventral margin.

No internal features could be seen.
Dimensions: Carapaces

|  | L | H | L/H | W |
| :--- | :---: | :---: | :---: | :---: |
| Female | 0.80 | 0.43 | I .86 | 0.38 |
| Male | 0.80 | 0.4 I | I .95 | 0.37 |

Discussion: $F$. lenijugum resembles $F$. plicatus (von Münster) with the lack of ornamentation between the longitudinal ridges. It differs in shape; $F$. plicatus has a more tapered posterior margin in lateral view. It also differs in the configuration of the ridges; the dorsal ridge does not form the dorsal margin in $F$. plicatus, nor does it join the anterior marginal rim; the ventral ridge is continuous with the anterior marginal rim, not merely joining it. F. lenijugum differs from all other described species by the absence of ornamentation between the ridges.

## Flexus schoelleri (Keij)

(Pl. 22, figs 6-8)
1955 Paracytheretta schoelleri Keij, p. 119, pl. 16, fig. 4; pl. 19, figs II-12.
1956 Cytheretta schoelleri (Keij) Oertli, p. 65, pl. 8, figs 196-197.
1965 Protocytheretta schoelleri (Keij) Moyes, p. 56, pl. 6, fig. 13.
1969 Protocytheretta schoelleri (Keij) Carbonnel, p. 1ıi, pl. 8, figs I-3.
Material: Couches du Phare: RO 269, ro valves and carapaces; RO 270, 5; RO 27r, 3. Io 4ri5-7. St. Geours-de-Maremne: ASG r, 3 valves and carapaces; ASG 2, 2; ASG 3, 2.

Type locality and horizon: Moulin de Gamachot, Upper Aquitanian (?).
Stratigraphical range and distribution: Couches du Phare, Biarritz; Faluns Bleues, St. Geours-de-Maremne; Aquitanian and Burdigalian of the Bordelais and Rhone.

Discussion: This was placed by Puri (1958) into his new genus Protocytheretta, defined as 'Cytheretta'-shaped, but with three longitudinal ridges; Flexus was regarded as being 'Cythereis' shaped and with three longitudinal ridges. F. schoelleri has a truncated posterior margin which is not at all 'Cytheretta'-like and the rodlike ridges are completely different from those of $P$. daniana (Brady). (See Hulings and Puri, 1964, p. 327 for an illustration of $P$. daniana.) $F$. schoelleri is probably not related to any other Flexus species here described, but is included in the genus on the purely morphological grounds that it has three longitudinal ridges.

The specimens from the Couches du Phare are smaller than the typical $F$. schoelleri (length of female carapace $=0.60$ compared with 0.78 ).

Flexus sp. A
(Pl. 22, fig. 5)
Material: i carapace. Io 4 II 8.
Locality and horizon: Bambrugge; Sables de Lede.
Dimensions: L, o.64; H, 0.36; W, 0.3I; L/H, i.78.
DISCUSSION: This is almost certainly a new species, but lack of material prevents a description. The configuration of the ridges is similar to $F$. concinnus (Triebel), but its shape is different from the latter both in dorsal and in lateral view, and it has a much stronger anterior marginal rim.

## XV. CONCLUSIONS

The Cytherettinae have proven useful for helping to establish a correlation between the various localities in the Anglo-Paris-Belgian area in the Eocene and between this region and Germany in the Oligocene. In particular they support the idea of correlating the Sables de Lede with the Upper Lutetian of the Paris Basin, placing the Sables moyens in the Middle Eocene and correlating them with the Upper Bracklesham Beds of Hampshire, and correlating the Barton Beds with the Marnes à P. ludensis. Unfortunately the Cytherettinae provide little information concerning the relationship of the type Lattorfian with other areas of western Europe. The four species recorded from the Headon Beds suggest a relationship with the Bartonian on the one hand ( $C$. porosacosta, $F$. ludensis) and with the Oligocene on the other (C. headonensis, C. aff. stigmosa), although the latter are related to the Eocene C. carita and C. cellulosa. Other ostracods however support a Bartonian age for the Headon Beds (Keen, 1968). Detailed correlation between England, France, and Belgium is possible using the evolution of C. costellata and C. laticosta.

The Aquitaine Basin formed a very distinct province, the only group in common with the northern areas being the C. eocaenica group. This suggests that the English Channel as now known could hardly have existed during the Eocene and Oligocene.

The presence of the Cytherettinae in Tertiary sediments is a good indication of shallow marine conditions, close to shore. Of the main species groups present, only the superspecies C. laticosta seems to have preferred muddy waters. The C. haimeana group were most abundant in clear waters in which calcareous or sandy sediments
were accumulating, the C. eocaenica, C. tenuipunctata, C. rhenana, and C. sagri groups inhabited clear waters where sands were being deposited.

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## PLATE I

## Cytheretta judaea (Brady)

Figs i, 4-7, 9. Specimens from Recent beach sand, Rimini.
Fig. i. Left valve, female, Io $3807 \times 70, \mathrm{~L}=0.75 \mathrm{~mm}$.
Fig. 4. Right valve, male, Io $3792, \times 100, \mathrm{~L}=0.79 \mathrm{~mm}$.
Fig. 5. Right valve, male, Io $3810, \times 70, \mathrm{~L}=0.79 \mathrm{~mm}$.
Fig. 6. Left valve, female, Io $3793, \times 70, \mathrm{~L}=0.75 \mathrm{~mm}$.
Fig. 7. Enlargement of Io $3810 \times 140$.
Fig. 9. Posterior radial pore canals of Io $3793, \times 100$.
Cytheretta subradiosa (Roemer)
Fig. 8. Right valve, male. Io $3795 \times$ ıoo, $L=0.8$ mm, Lower Pliocene, Rimini.

# BULLETIN OF <br> THE BRITISH MUSEUM (NATURAL HISTORY) GEOLOGY 

## CORRIGENDA

Plate 2, caption to Fig. 8
For "punctuation" read "punctation".

Plate 15, caption to Fig. Io For "Io 4031" read "Io 4030".

Plate 19, caption to Fig. 5-7,9
For "Calcaire a Algues" read "Calcaire à Algues".


## PLATE 2

All, except figs. $7,8, \times 70$
Figs. 1-10 Cytheretta costellata costellata (Roemer)
Fig. 5 from Sables de Lede, Bambrugge; Fig. 6 from Upper Bracklesham Beds, Selsey; remainder from Lutetian IV, Damery. All except Fig. 5 are MORPHOTYPE A.

Fig. I Left valve, female, Io $3796, \mathrm{~L}=0.69 \mathrm{~mm}$.
Fig. 2 Left valve, male, Io $3798, \mathrm{~L}=0.72 \mathrm{~mm}$.
Fig. 3 Right valve, female, Io $3797, \mathrm{~L}=0.69 \mathrm{~mm}$.
Fig. 4 Right valve, male, Io $3799, \mathrm{~L}=0.72 \mathrm{~mm}$.
Fig. 5 Left valve, female, Io $3802, \mathrm{~L}=0.72 \mathrm{~mm}$. MORPHOTIPE B.
Fig. 6 Left valve, female, Io $3803, \mathrm{~L}=0.64 \mathrm{~mm}$.
Fig. 7 Detail of Io 3797, $\times 140$
Fig. 8 Detail of Io 3797 showing "punctuation" between the ridges, $\times 300$
Fig. 9 Female carapace, dorsal view, lo $3800, L=0.70 \mathrm{~mm}$.
Fig. io Male carapace, ventral view, Io $380 \mathrm{I}, \mathrm{L}=0.75 \mathrm{~mm}$.


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## PLATE 3 <br> All, except Fig. 8, $\times 75$

Fig. I-8 Cytheretta costellata grandipora subsp. nov.
Fig. I MORPHOTYPE C, Left valve male, Io $3812, L=0.83$ Auvers-en-Oise.
Fig. 2 MORPHOTYPE, E. Right valve, female, Io 38 i i, L $=0.74$ Auvers-en-Oise.
Fig. 3 MORPHOTYPE, D, Left valve, male, Io $3809, L=0.83$ Auvers-en-Oise.
Fig. 4 MORPHOTYPE, E, Right valve, female, Io $3805, \mathrm{~L}=0.77$ Moiselles.
Fig. 5 MORPHOTYPE, D, Left valve, female, Io $3808, \mathrm{~L}=0.74$ Auvers-en-Oise.
Fig. 6 MORPHOTYPE, E, Right valve, male, Io $3807, L=0.85$ Moiselles.
Fig. 7 MORPHOTYPE E, Left valve, female, Io $38 \mathrm{o}_{4}$, $\mathrm{L}=0.76$ Moiselles. HOLOTYPE
Fig. 8 Enlargement of Io 3804 showing " pores ". $\times 150$.

Fig. 9 Cytheretta bambruggensis Keij. Right valve, female, Io $3827, \mathrm{~L}=0.74$. Sables de Lede, Bambrugge.

Fig. io Cytheretta sp. C. Right valve, female, $L=0.70$ Auvers-en-Oise. Specimen destroyed.


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## PLATE 4 <br> $\times 75$

Fig. I-8 Cytheretta costellata cratis subsp. nov. All specimens are MORPHOTYPE F from the Marnes à $P$. ludensis, Verzy.

Fig. I Left valve, female, Io $3^{81} 4, L=0.73$ HOLOTYPE
Frg. 2 Left valve, male, Io $3817, L=0.76$
Fig. 3 Right valve, female, Io $3^{815}, \mathrm{~L}=0.70$
Fig. 4 Right valve, male, Io $3818, L=0.83$
Fig. 5 Left valve, larval no. 8, Io $3820, \mathrm{~L}=0.60$
Fig. 6 Right valve, larval no. 8, Io 38i9, $L=0.60$
Fig. 7 Female carapace, ventral view, Io $3816, L=0.73$
Fig. 8 Male carapace, dorsal view, Io $382 \mathrm{I}, \mathrm{L}=0.76$
Fig. 9-II Cytheretta costellata antecalva subsp. nov. All specimens are MORPHOTYPE G from the Middle Barton Beds, Barton.

Fig. 9 Left valve, male, Io $3825, \mathrm{~L}=0.84$
Fig. io Left valve, female, Io $3823, L=0.77$. HOLOTYPE.
Fig. il Right valve, female, Io $3824, L=0.77$


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## PLATE 5

Fig. 1-3 Cytheretta costellata cratis subsp, nov.
Fig. I Right valve, female, Io $3822, \mathrm{~L}=0.67, \times 80$, showing the inner margin. From the Marnes à $P$. ludensis, Chavençon.
Fig. 2 Hinge of Io 3822. $\times 400$
Fig. 3 Central muscle scars and fulcral point of Io 3822. $\times 800$.

Fig. 4-7 Cytheretta ruelensis subsp, nov. Io 3837 , Sables de Cresnes, Le Ruel. $\times$ 8o. Female carapace. HOLOTYPE.

Fig. 4 Posterior view
Fig. 5 Dorsal view
Fig. 6 Left valve
Fig. 7 Right valve


## PLATE 6 <br> All $\times 70$

Fig. i, 6 Cytheretta haimeana (Bosquet)
Fig. I Left valve, female, Io $3834, \mathrm{~L}=0 \cdot 60$. Lutetian IV, Damery.
Fig. 6 Left valve, female, Io $3835, \mathrm{~L}=0 \cdot 70$. Sables de Beauchamp, Moiselles.
Fig. 2,5 Cytheretta crassivenia Apostolescu.
Fig. 2 Left valve, female, Io $3828, \mathrm{~L}=0 \cdot 66$. Lutetian IV, Damery.
Fig. 5 Left valve, female, Io $3829, \mathrm{~L}=0 \cdot 70$. Sables de Beauchamp, Moiselles.
Fig. 3 Cytheretta aff. decipiens Keij
Left valve, female, of a carapace Io $3833, \mathrm{~L}=0.66$. Marnes à $P$. ludensis, Chavençon.

Fig. 4, 7 Cytheretta ruelensis sp. nov.
Fig. 4 Ventral view of male carapace, Io $3838, L=0.85$. Sables de Cresnes, Le Ruel.
Fig. $7 \quad$ Left valve of Io 3838 .
Fig. 8-Io Cytheretta decipiens Keij
Specimens from Sables de Beauchamp. Moiselles.
Fig. 8 Left valve, female, Io $3830, \mathrm{~L}=0.69$
Fig. 9 Left valve, male, Io $3832, \mathrm{~L}=\mathrm{o} \cdot 8 \mathrm{I}$
Fig. io Right valve, female, Io $3831, \mathrm{~L}=0.73$
Fig. II Cytheretta sp. A
Left valve, $\mathrm{Io} 4092, \mathrm{~L}=0.74$. Sables de Beauchamp, Moiselles.



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## PLATE 7

## Cytheretta eocaenica Keij

Fig. 6 from Lutetian IV, Damery; remainder from Sables de Lede, Bambrugge.
Fig. i Left valve, female, lo $384 \mathrm{I}, \times 65, \mathrm{~L}=0.79$
Fig. 2 Left valve, male, Io $3844, \times 65, \mathrm{~L}=0.88$
Fig. 3 Left valve, female, Io $3840, \times 65, \mathrm{~L}=0.88$
Fig. 4 Hinge of lo $3844, \times 125$
Fig. 5 Central muscle scars of Io $3^{84} 4, \times 250$
Fig. 6 Left valve, female, Io $3839, \times 65, \mathrm{~L}=0.80$
Fig. 7 Right valve, male, Io $384^{2}, \times 65, \mathrm{~L}=0.83$
Fig. 8 Anterior tooth and hinge bar of fo $3^{8} 44, \times 650$
Fig. 9 Left valve, female, lo $3843, L=0 \cdot 93$. Post-maturation moult stage.
Fig. io Detail of pitting of Io $3839, \times 750$.


## PLATE 8

## Cytheretta oligocaenica sp. nov.

Specimens of Fig. I, 2, 4 from the Couches du Phare, Biarritz; specimen of remaining Fig. from Faluns Bleues. St. Geours-de-Maremne.

Fig. I Left valve, female, Io $3845, \times 70, \mathrm{~L}=0.85$, HOLOTYPE
Fig. 2 Carapace, dorsal view, male, Io $3847, \times 70, \mathrm{~L}=0.86$
Fig. 3 Central muscle scars of Io 3849
Fig. 4 Right valve, female, Io $3846, \times 70, \mathrm{~L}=0.84$
Fig. 5 Right valve, female, Io $3849, \times 100, \mathrm{~L}=0.84$
Fig. 5 Right valve, female, Io $3849, \times 100, \mathrm{~L}=0.84$
Fig. 6 Hinge of Io $38 \mathbf{4 9}, \times 125$
Fig. 7 Io $3849, \times 70$
Fig. 8 Anterior tooth of Io 3849 , from dorsal, $\times 350$
Fig. 9 Anterior tooth of Io 3849, from anterior, $\times 350$
Fig. io Anterior tooth of Io 3849 , from lateral view, $\times 350$
Fig. II Posterior tooth of Io 3849 , from ventral, $\times 350$
Fig. 12 Posterior tooth of Io 3849 , from posterior, $\times 35^{\circ}$
Fig. I3 Posterior tooth of Io 3849 , from lateral view, $\times 350$.


## PLATE 9 <br> All $\times 70$

Fig. 1-4, 6, 7 Cytheretta cellulosa sp. nov.
Fig. 2 from Sables de Beauchamp, Moiselles; remainder from Sables d'Auvers-en-Oise.

Fig. I Left valve, female, Io $3859, \mathrm{~L}=0.78$; HOLOTYPE
Fig. 2 Right valve, female, Io 3860 , $\mathrm{L}=0.74$
Fig. 3 Left valve, male, Io $386 \mathrm{I}, \mathrm{L}=0.96$
Fig. 4 Male carapace, dorsal view, Io 3863 , $\mathrm{L}=0.93$
Fig. 6 Right valve, male, Io $3862, \mathrm{~L}=0.93$
Fig. 7 Posterior view of Io 3863.
Fig. 5, 8, 9-II Cytheretta carita sp. nov.
Specimens from the Sables de Beauchamp, Moiselles.
Fig. 5 Female carapace, dorsal view, $\mathrm{L}=0.87$; specimen destroyed
Fig. 8 Female carapace, anterior view; specimen destroyed
Fig. 9 Left valve, female, Io $3853, L=0.89$; HOLOTYPE
Fig. io Right valve, female, Io $3854, \mathrm{~L}=0.85$
Fig. 1 I Left valve, male, Io $3855, \mathrm{~L}=0.94$
Fig. 12 Cytheretta sp. B
Right valve, Io 4093; Marnes à Pentacrinus, Biarritz.


Cytheretta geoursenis sp. nov.
Specimens from the Faluns bleues, St. Geours-de-Maremne.
Fig. I Left valve, male, Io $3852, \times 70, \mathrm{~L}=1.07$
Fig. 3 Left valve, female, Io $3850, \times 60, L=0.98$; HOLOTYPE
Fig. 5 Right valve, female, Io $385 \mathrm{I}, \times 70, \mathrm{~L}=0.93$

Fig. 2, 4, 6, 8, 9, Cytheretta laticosta (Reuss)
Specimens from the Middle Barton Beds, Barton.
Frg. 2 Left valve, female, Io $3865, \times 70, L=0.77$
Fig. 4 Left valve, male, Io $3864, \times 70, L=0.90$
Fig. 6 Right valve, male, Io $3866, \times 70, L=0.90$
Fig. 8 Enlargement of Io 3864 , central area between ventral and medium ridges, showing punctation. $\times 250$.
Fig. 9 Further enlargement of Io 3864 , showing a normal pore canal and surrounding puncta. $\times 850$.

Fig. 7 Cytheretta carita sp. nov.
Male carapace, ventral view, Io $3858, \times 70, L=0.93$; Sables de Beauchamp, Moiselles.


# PLATE II <br> $\times 70$, except Fig. 7 

FIG. I-4, 8, 9 Cytherettaforticosta sp. nov.
Fig. I-4 from Upper Bracklesham Beds, Whitecliff Bay
Fig. I Left valve, female, Io $3871, L=0.79$; HOLOTYPE
Fig. 2 Left valve, male, Io $3872, L=0.87$
Fig. 3 Right valve, female, Io $3874, \mathrm{~L}=0.84$
Fig. 4 Right valve, male, Io $3873, L=0.91$
Fig. 8 Female carapace, ventral view, Io $3875, L=0.80$; Upper Bracklesham Beds, Selsey.
Fig. 9 Male carapace, dorsal view, Io $3876, L=0.92$; Upper Bracklesham Beds, Selsey.

Fig. 5-7 Cytheretta porosacosta sp. nov.
Fig. 5 Left valve, male, Io $3880, \mathrm{~L}=0.79$ Middle Headon Beds, Colwell Bay.
Fig. 6 Left valve, female, Io $3879, L=0.75$. HOLOTYPE; Middle Headon Beds, Colwell Bay.
Fig. 7 Enlargement of Io 3880 showing punctation $\times 140$.


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## PLATE 12

Fig. I-2, 5 Cytheretta laticosta (Reuss)
Specimens from Middle Barton Beds, Barton; $\times 70$.
Fig. 1 Male carapace, ventral view; Io 3869, $L=0.88$
Fig. 2 Female carapace, dorsal view, Io $3868, L=0.77$
Fig. 5 Left valve, female, Io $3869, L=0.81$

Fig. 3, 4 Cytheretta porosacosta sp. nov.

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\times 70
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Fig. 3 Right valve, male, Io 3882, L $=0.81$; Middle Headon Beds, Milford.
Fig. 4 Right valve, female, Io $388 \mathrm{r}, \mathrm{L}=0.76$; Middle Headon Beds, Milford.

Fig. 6-12 Cytheretta forticosta sp. nov.
Fig. 6 Right valve, female, Io $3878, \times 70, \mathrm{~L}=0 \cdot 86$; Upper Bracklesham Beds, Selsey.
Fig. 7 Dorsal muscle scars, $\times 350$
F1G. 8 Posterior duplicature, $\times 350$
Fig. 9 Anterior tooth, $\times 350$
Fig. Io Posterior tooth, dorsal view, $\times 35^{\circ}$
Fig. II Anterior tooth, dorsal view, $\times 35^{\circ}$
Fig. 12 Central muscle scars, $\times 350$.


## PLATE 13

Cytheretta tenuistriata ornata subsp. nov.
Fig. I Left valve, female, Io $3898, \mathrm{~L}=\mathrm{I} \cdot 03, \times 50$; HOLOTYPE
Fig. 2 Right valve, male, Io 402I, L $=\mathrm{I} \cdot \mathrm{I} 4, \times 50$
Fig. 3 Right valve, female, Io $3899, L=\mathrm{I} \cdot{ }^{\circ} 2$
Fig. 4 Left valve, female; specimen destroyed
Fig. 5 Left valve, male, Io $4020, \mathrm{~L}=\mathrm{I} \cdot \mathrm{I} 5$
Fig. 6 Right valve, male; specimen destroyed
FIG. 7 Left valve, 8 th moult stage, $L=0.87$; specimen destroyed
Fig. 8 Right valve, 8 th moult stage, 10 4025, $L=0.86$
Fig. 9 Left valve, 7 th moult stage, $\mathrm{L}=75^{\circ}$; specimen destroyed
Fig. io Right valve, 7 th moult stage, Io $4026, \mathrm{~L}=0.80$
Fig. II Left valve, 6 th moult stage, Io $4024, \mathrm{~L}=0.58$
Fig. I2 Right valve, 6 th moult stage, Io $4027, \mathrm{~L}=0.59$
Specimens from the Falun d'Auvers-St.-Georges.


## PLATE 14

Cytheretta tenuipunctata absoluta subsp. nov.
Fig. 1-4, 6, 7; $\times 60$; specimens from the Marnes à Huitres, Cormeilles.
Fig. I Left valve, female, Io $3884, \mathrm{~L}=0.84$; HOLOTYPE
Fig. 2 Left valve, male, Io $3886, \mathrm{~L}=0.98$
Fig. 3 Right valve, female, Io $3885, \mathrm{~L}=0.87$
Fig. 4 Right valve, male, Io 3887 , $\mathrm{L}=0.98$
Fig. 6 Female carapace, dorsal view, Io $3888, L=0.90$
Fig. 7 Male carapace, ventral view, Io 3889 , $L=0.98$.
Cytheretta tenuipunctata lirata subsp. nov.
Fig. 5, 8-10, $\times 50$; specimens from the Falun d'Auvers-St.-Georges.
Fig. 5 Left valve, female, Io $3890, L=0.90$; HOLOTYPE
Fig. 8 Right valve, female, $L=0.90$; specimen destroyed
Fig. 9 Right valve, male, Io $3893, \mathrm{~L}=\mathrm{I} \cdot 01$
Fig. io Left valve, male, Io $3892, L=1.04$.


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PLATE I5
$\times 60$, except Fig. $9, \times 50$
Cytheretta buttensis reticulata sp. nov., subsp. nov.
Fig. i-8, Specimens from Cormeilles.
MORPHOTYPE A.
Fig. I Left valve, female, Io 4032, $\mathrm{L}=0.85$, Marnes à Huitres; HOLOTYPE
Fig. 2 Left valve, male, Io 4033, L $=0.97$, Marnes à Huitres.
Fig. 3 Right valve, female, Io $4038, L=0.82$, Couches de Sannois
Fig. 4 Female carapace, dorsal view, Io $4034, L=0.91$, Marnes à Huitres
Fig. 5 Male carapace, dorsal view, $L=0 \cdot 95$, Marnes à Huitres. Specimen destroyed.

## MORPHOTYPE B

Fig. 6 Right valve, female, $L=0.83$, Couches de Sannois, Io 4036
Fig. 7 Left valve, female, Io $4037, L=0 \cdot 88$, Couches de Sannois.
MORPHOTYPE C
Fig. 8 Right valve, male, Io 4035, $L=0.96$, Couches de Sannois

Cytheretta buttensis buttensis sp. nov.
Fig. io Left valve, male, Io 403I, L = o.9i, MORPHOTYPE C, Couches de Sannois; HOLOTYPE

Cytheretta tenuipunctata lirata subsp. nov.
Fig. 9 Right valve, female, $L=0.90$; specimen destroyed.


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## Cytheretta minipunctatasp. nov.

Fig. I-3, $\times 50$. Specimens from the Couches de Sannois, Cormeilles
Fig. i Left valve, male, Io $4028, \mathrm{~L}=\mathrm{i} \cdot \mathrm{Io}$. HOLOTXPE
Fig. 2 Male carapace, ventral view, Io 4028
Fig. 3 Female carapace, ventral view, Io $4029, L=0.98$.

Cytheretta tenuipunctata lirata subsp. nov.
Fig. 4 Left valve, male, Io $3894, L=1 \cdot 0_{4}, \times 55$; Falun d'Auvers-St.-Georges.

Cytheretta tenuistriata tenuistriata (Reuss).
Fig. 5, 7 Specimens from the Unterer Meeresand, Alzey Trift
Fig. 5 Left valve, male, Io $3896, L=1 \cdot 25, \times 40$
Fig. 7 Right valve, female, Io $3897, L=I \cdot 10, \times 50$.

Cytheretta minor (Lienenklaus).
Fig. 6 Left valve, female, Io $3704, L=0.88$; Unt. Meeresand, Alzey Trift, $\times 60$.

Cytheretta aff. stigmosa Triebel.
Fig. 8 Left valve, female, Io 4052, $\mathrm{L}=0.76, \times 65$; Mid. Headon Beds, Whitecliff Bay.

Cytheretta gibberis sp. nov.
Fig. 9, 10, $\times 70$ Specimens from the Couches du Phare, Biarritz
Fig. 9 Right valve, male, Io $4086, L=0.92$
Fig. io Right valve, female, Io $4084, \mathrm{~L}=0.88$; HOLOTYPE.


## PLATE I 7

Cytheretta stigmosa gallica subsp. nov.
Fig. I, 2, io Specimens from the Falun d'Auvers-St.-Georges, $\times 60$
Fig. I Left valve, female, Io 4053, $\mathrm{L}=0.75$; HOLOTYPE
Fig. 2 Left valve, male, Io 4055, $L=0.73$
Fig. 5 Female carapace, dorsal view, $L=0.73$; specimen destroyed
Fig. io Male carapace, dorsal view, Io 4056, $L=0.74$.

Cytheretta regularis sp. nov.
Fig. 3, 4, 5, 6, 7 Specimens from the Stampian of Gaas (Lesbarritz), $\times 60$
Fig. 3 Left valve, female, Io 4057, $L=0.70$; HOLOTYPE
Fig. 4 Right valve, female, Io $4058, L=0.68$
Fig. 6 Left valve, male, Io 4059, $L=0.70$
Fig. 7 Right valve, male, Io $4060, \mathrm{~L}=0.68$.

Cytheretta vesca sp. nov.
Fig. 8, 9, 12 Specimens from the Falun d'Auvers-St.-Georges, $\times 60$
Fig. 8 Left valve, female, Io $4048, L=0.73$; HOLOTYPE
Fig. 9 Right valve, male, Io 4051, $L=0.71$
Fig. 12 Right valve, female, Io 4049, L $=0.72$.
Cytheretta headonensis Haskins.
Fig. il, I3, 14 Specimens from the Middle Headon Beds, $\times 50$
Fig. 11 Right valve, male, Io 4044, L $=0.80$; Milford
Fig. 13 Left valve, male, Io 4043, L =0.78; Headon Hill
Fig. 14 Right valve, female, Io 4046, $\mathrm{L}=0.80$; Headon Hill.


## PLATE I 8

Cytheretta posticalis parisiensis subsp. nov.
Fig. I-4, 6 Specimens from the Falun d'Auvers-St.-Georges
Fig. 1 Left valve, female, Io $4039, \mathrm{~L}=0.95, \times 50$; HOLOTYPE
Fig. 2 Left valve, male, Io $404 \mathrm{I}, \mathrm{L}=\mathrm{I} \cdot \mathrm{o}_{5}, \times 50$
Fig. 3 Right valve, female, Io 4040, L $=0.91, \times 50$
Fig. 4 Right valve, male, Io $4042, L=I \cdot 03, \times 50$
Fig. 6 Anterior radial pore canals of left valve, Io 3702, $\times 110$.

Cytheretta bullans sp. nov.
Fig. 5, 7, $\times 70$ Specimens from the Calcaire à Algues, Blaignan
Fig. 5 Left valve, female, Io $406 \mathrm{I}, \mathrm{L}=0.85$; HOLOTYPE
Fig. 7 Right valve, male, Io 4062, L $=0.90$.

Cytheretta rhenana Triebel.
Fıg. 8 Left valve, female, Io 4047, $L=0.87, \times 60$; Unt. Meeresand, Alzey Trift.

## Cytheretta headonensis Haskins.

Fig. 9 Left valve, female, Io $4045, \mathrm{~L}=0.83, \times 70$; Mid. Headon Beds, Headon Hill.


## PLATE 19 <br> $\times 75$

Cytheretta sagri sagri Deltel.
Fig. I-4 Specimens from the Stampian of Gaas
MORPHOTYPE A, Gaas (Espibos)
Fig. I Left valve, female, Io $4063, L=0.84$
Fig. 2 Right valve, male, Io $4066, \mathrm{~L}=0.90$
Fig. 3 Right valve, female, Io $4064, L=0.84$.
MORPHOTYPE D, Gaas (Lesbarritz)
Fig. 4 Left valve, female, Io $4076, L=0.92$.

Cytheretta sagri inconstans subsp. nov.
Fig. 5-7, 9 Specimens from the Calcaire a Algues, Blaignan.
MORPHOTYPE C
Fig. 5 Left valve, male, Io 4069, $L=0.95$
Fig. 6 Left valve, female, Io $4070, L=0.95$.
MORPHOTYPE B
Fig. 7 Left valve, female, Io $4067, L=0.78$; HOLOTYPE
Fig. 9 Female carapace, dorsal view, Io 4067.

Cytheretta perita Deltel.
Fig. 8 Left valve, female, Io 4089, $L=0.8 \mathrm{I}$; Bartonian of Le Vigneau.

Cytheretta gibberis sp. nov.
Fig. io Female carapace, dorsal view, Io $4085, L=0.86$; Couches du Phare, Biarritz.


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## PLATE 20

$\times 75$
Cytheretta sagri martini subsp. nov.
Fig. I-4 Specimens from the Couches du Phare, Biarritz
MORPHOTYPE E
Fig. I Left valve, female, Io 4071, L $=0.83$; HOLOTYPE
Fig. 2 Right valve, female, Io $4072, L=0.8 \mathrm{I}$
Fig. 3 Left valve, male, Io $4073, L=0.86$.
MORPHOTYPE $F$
Fig. 4 Left valve, male, Io $4074, \mathrm{~L}=0.87$.

Cytheretta postornata sp. nov.
Fig. 5-8 Specimens from the Couches de l'Atalaye, Biarritz
Fig. 5 Left valve, male, Io $4088, \mathrm{~L}=0.84$
Fig. 6 Right valve, female, Io $4087, L=0.83$; HOLOTYPE
Fig. 7 Right valve, male, Io 4088
Fig. 8 Left valve, female, Io 4087.

## Cytheretta sculpta Ducasse.

Fig. 9, 10 Specimens from the Argiles à Algues, Blaignan
Fig. 9 Right valve, male, Io 4091, L $=0.73$.
Fig. 10 Left valve, female, Io $4090, L=0 \cdot 70$.

$9 \quad 10$


## PLATE 2 I

$\times 70$, except Fig. 5 which is $\times 160$
Cytheretta minipustulosa sp. nov.
Fig. I-4 Specimens from the Couches du Phare, Biarritz
Fig. I Right valve, male, Io 4080, L = I 09 ; HOLOTYPE
Fig. 2 Right valve, female, Io 4082, $L=0.98$
Fig. 3 Male carapace, dorsal view, Io 408I, L = I.00
Fig. 4 Left valve, female, Io $4083, L=0.88$.
Cytheretta samothracia Deltel.
Fig. 5, 6, 8 Specimens from the Couches du Phare, Biarritz
Fig. 5 Enlargement of the antero-dorsal area of Io 4077
Fig. 6 Left valve, female, Io 4077, $L=0.95$
Fig. 8 Left valve, male, Io $4078, \mathrm{~L}=\mathrm{I} \cdot \mathrm{O}_{4}$.

Flexus lenijugum sp. nov.
Fig. 7, 9 Specimens from the Argiles à Algues, Blaignan
Fig. 7 Left valve, male, Io $4^{1 I} 4, L=0.80$
Fig. 8 Right valve, female, Io $4113, L=0.80$; HOLOTYPE.



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## PLATE 22 <br> $\times 60$

Flexus plicatus (von Munster).
Fig. I Left valve, Io 4094, $\mathrm{L}=0.80$; Chattian, Astrup.

Flexus concinnus (Triebel).
Fig. 2, 3
Fig. 2 Left valve, male, Io 4095, $\mathrm{L}=0.94$; Unt. Meeresand, Alzey Trift
Fig. 3 Left valve, male, Io 4096, L $=0.81$; Falun d'Auvers-St.-Georges

Flexus sp. A
Fig. 5 Left valve, female, Io $4 \mathrm{II} 8, L=0.7 \mathrm{I}$; Sables de Lede, Bambrugge.

Flexus gutzwilleri (Oertli).
Fig. 4 Left valve, female, Io 4098 , $L=0.79$; Couches du Phare, Biarritz.

## Flexus schoelleri (Keij).

Fig. 6-8 Specimens from the Faluns bleues, St. Geours-de-Maremne
Fig. 6 Left valve, female, Io 4 II $5, L=0.71$
Fig. 7 Left valve, male, Io 4iI7, $L=0.74$
Fig. 8 Right valve, female, Io $4116, L=0.71$.

Flexus lenijugum sp. nov.
Fig. 9, Io Specimens from the Argiles à Algues, Blaignan
Fig. 9 Male carapace, dorsal view, Io 4 II4, $L=0.80$
Fig. io Female carapace, dorsal view, Io $4 \mathrm{II} 3, \mathrm{~L}=0.80$; HOLOTYPE

Cytheretta bullans sp. nov.
Fig. 1 I Female carapace, dorsal view, Io $406 \mathrm{I}, \mathrm{L}=0.85$; HOLOTYPE. Calcaire à Algues, Blaignan.

Cytheretta postornata sp. nov.
Fig. 12 Female carapace, dorsal view, Io $4087, L=0.83$; HOLOTYPE. Couches de l'Atalaye, Biarritz.


## PLATE 23 <br> $\times 70$

Flexus ludensis sp. nov.
Fig. I-6, 16 Specimens from the Marnes à P. ludensis, Verzy, except Fig. 6
Fig. I Left valve, female, Io $4106, L=0.50$; HOLOTYPE
Fig. 2 Left valve, male, Io $4107, L=0.52$
Fig. 3 Right valve, male, Io 4III, L $=0.5$ I
Fig. 4 Male carapace, ventral view, Io 4 IO9, $L=0.52$
Fig. 5 Right valve, female, Io 4 IIo, $L=0.5 \mathrm{I}$
Fig. 6 Left valve, male, Io 4 II2, $L=0.55$; Mid. Headon Beds, Whitecliff Bay
Fig. i6 Female carapace, dorsal view, Io 4 Io8, $L=0.50$.

Flexus solentensis solentensis sp. nov.
Fig. 7-10 Specimens from the Middle Barton Beds
Fig. 7 Female carapace, dorsal view, Io $4101, L=0.54$; Alum Bay
Fig. 8 Left valve, Io 4 ioi
Fig. 9 Right valve, female, $L=0.5 \mathrm{I}$; Barton; specimen destroyed
Fig. 10 Left valve, male, Io $4100, \mathrm{~L}=0.54$; Barton; HOLOTYPE.

Flexus solentensis congestus subsp. nov.
Fig. II-I5 Specimens from the Upper Barton Beds, Barton
Fig. 1 I Left valve, female, Io 4 IO3, $L=0.5$ i ; HOLOTYPE
Fig. 12 Male carapace, ventral view, $\mathrm{Io}_{4} \mathrm{IO}_{4}, \mathrm{~L}=0.54$
Fig. 13 Left value, Io 4 ro4
Fig. If Right valve, female, Io $4105, L=0.5 \mathrm{I}$
Fig. I5 Male carapace, anterior view, Io 4 Io4.


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